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BY
W. H. PEARSALL

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WITH TWENTY-SIX PLATES, AND NUMEROUS
FIGURES IN THE TEXT



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ECOLOGICAL STUDIES ON THE RAIN FOREST OF SOUTHERN NIGERIA

I. THE STRUCTURE AND FLORISTIC COMPOSITION OF THE PRIMARY FOREST

By P. W. RICHARDS
Botany School, Cambridge

(With Plates I and II and seven Figures in the Text)

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I. INTRODUCTION

THE present paper, which forms the first part of the results of the Cambridge Botanical Expedition to Nigeria, is a description of a typical region of the West African Rain Forest. Its chief object is to compare the Rain Forest of this area with that previously studied by the author in British Guiana (Davis & Richards, 1933-4) and Sarawak (Richards, 1936). In order that the comparison should be objective and exact, an effort has been made to give quantitative data whenever possible.

2 *Ecological studies on the Rain Forest of Southern Nigeria*

The author wishes to take the opportunity of thanking the Percy Sladen Trustees, the Government Grant Committee of the Royal Society, the Worts Fund of Cambridge University and the Rouse Ball Fund of Trinity College, Cambridge, for the financial help which made the expedition possible. It is also a great pleasure to thank the late Director of Forests, Nigeria (Mr J. R. Ainslie), and various members of his staff for their hospitality and also for many facilities and much friendly assistance. The author is also indebted to Sir Arthur Hill, K.C.M.G., F.R.S., Dr J. Ramsbottom, O.B.E., and Sir Albert Seward, F.R.S., for kind help and encouragement in organizing the expedition. Mr W. J. F. Campbell, formerly of the School of Rural Economy, Oxford, a member of the expedition, has very kindly allowed the author to use the unpublished results of his soil analyses in preparing this paper. Finally, a word of thanks is due to Forest Guard J. Osseyemeh, without whose knowledge and patient assistance the results described here could not have been obtained.

The collection of plants on which these "Studies" are based was made by Mr R. Ross and the author, and the first set of specimens is deposited in the herbarium of the British Museum (Natural History). Except for the genera *Pausinystalia* and *Scottellia*, and the Orchidaceae, which were kindly determined by Mr A. C. Hoyle (School of Forestry, Oxford), Dr H. Sleumer (Berlin-Dahlem) and Mr V. S. Summerhayes (Kew), respectively, all the flowering plants and ferns were identified by the staff of the Botanical Department of the British Museum, to whom grateful thanks are due. The bryophytes have been identified by the author. In the text of this paper and in Tables III and VI-IX the numbers in brackets after names of species are the collector's numbers attached to the specimens: numbers from 1 to 300 are Mr Ross's collecting numbers, those from 3000 upwards are those of the author. Where no number is quoted, the identification was made in the field with the help of the *Flora of West Tropical Africa*, vol. 1 and vol. 2, pt. 1 (Hutchinson & Dalziel, 1931). The sign * against a number indicates that the specimen in question was collected actually on the sample or clear-felling plot or from the tree under consideration. Identifications not based on material collected by us are given only for very distinct and unmistakable species.

GENERAL DESCRIPTION OF REGION

Southern Nigeria west of the Niger, the part of the country with which we are alone concerned, lies between 4° and 9° N. lat. It is a sloping, gently undulating plain and, except for occasional isolated, steep-sided hills ("inselbergs"), it has no striking features of relief, though it is nowhere a dead level. At about 100-150 miles (160-240 km.) from the coast it reaches an average elevation of about 1200 ft. (360 m.): from there it falls gradually, on the north and east towards the Niger, on the south and west towards the narrow swampy strip bordering the coast.

The underlying rocks of the whole region are a crystalline complex of Pre-Cambrian age. Towards the north this outcrops in many places, but southwards it is covered by a considerable thickness of Tertiary deposits, including the Benin Sands. The swampy coastal strip is formed of alluvium.

The average rainfall over the whole area is high, and the rivers draining it are many and of some size. From west to east the chief are the Ogun, the

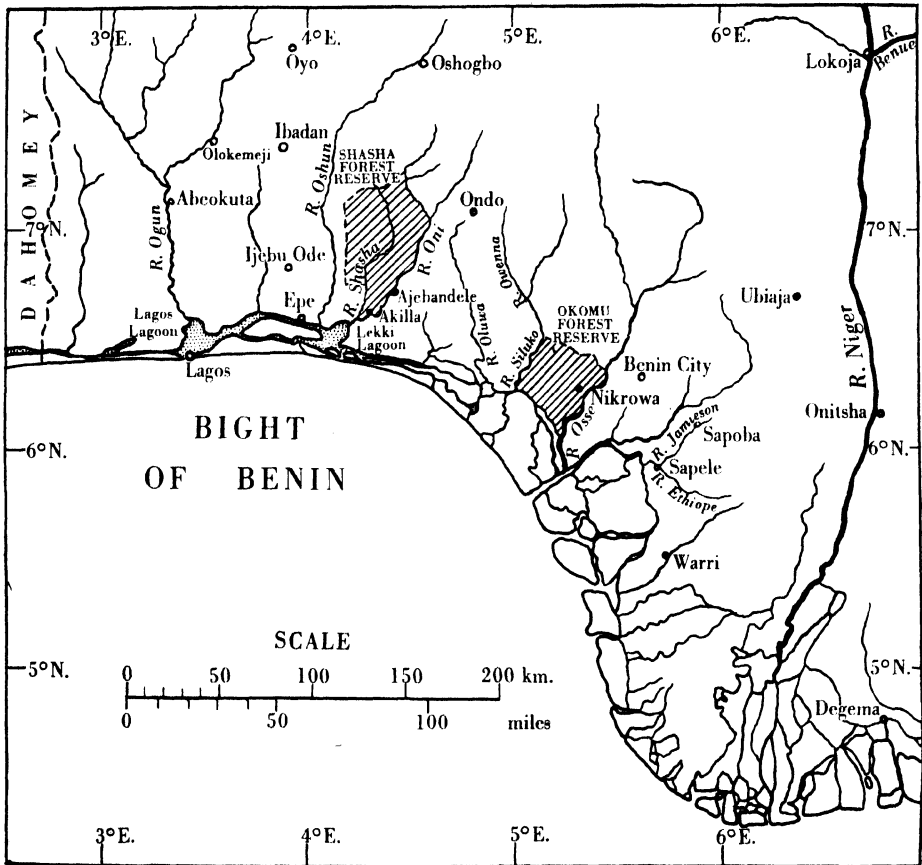


FIG. 1. Sketch-map of south-western Nigeria, to show the position of the Shasha and Okomu Forest Reserves (other forest reserves not shown).

Oshun, the Oni, with its tributary the Shasha (or Omo), the Owenna and the Osse. None of these rivers flows directly into the sea: they discharge into a chain of narrow lagoons and anastomosing waterways which runs along the coast the entire distance from the Niger delta to the western frontier and on into Dahomey. These lagoons are separated from the sea by a sand-bar often less than a mile wide: mostly they are fresh or brackish.

4 *Ecological studies on the Rain Forest of Southern Nigeria*

The distribution of vegetation in West Africa depends chiefly on the fact that the climate becomes more or less steadily drier with increasing distance from the sea. The climatic climaxes therefore form zones running roughly parallel to the coast and widening or narrowing as the local orographic factors alter the steepness of the climatic gradient. Three of these zones cross the region under consideration, viz. the Rain Forest Zone, the Mixed Deciduous Forest Zone and the Parkland Zone. The first and second of these are undoubted climatic climax zones, but recent work makes it likely that part at least of the apparently climax vegetation of the third is a subclimax derived from the second by human influence and kept stable by annual bush-fires (MacGregor, 1937).

In south-western Nigeria the Rain Forest Zone is more than 60 miles (100 km.) wide¹ in its widest part in Benin Province and becomes narrower towards the west. As a large part of its width is occupied by mangrove and freshwater swamp forests (edaphic climaxes), the Rain Forest Zone in the strict sense is very narrow. At the present time, however, the area of rain forest has been so reduced by cultivation and exploitation that the existing rain forest forms a series of disconnected blocks rather than a continuous belt.

The whole of Southern Nigeria is relatively thickly populated and in an advanced state of economic development. The density of population varies from 235 per sq. mile in the Colony and 125 in Ijebu to 56 in Ondo. Ibadan (in the Parkland Zone), with over 200,000 inhabitants, is one of the largest native towns in Africa. The most important native tribes are the Yorubas and Binis.

Since the population is so large it is not surprising that a very large proportion of the area is farmed. There are few large European plantations and nearly all the agriculture is of an extremely primitive type, usually some form of shifting cultivation. The most important crops are the oil palm (*Elaeis guineensis* Jacq.) and cacao (*Theobroma Cacao* L.), but many other crops are grown both for subsistence and for export.

Nearly all considerable areas of Rain Forest and Mixed Deciduous Forest in south-western Nigeria are now forest reserves under the control of either the central government or the local native administrations. In most of these reserves timber is exploited on a large scale, but may only be cut under permit: farming is not allowed except in certain definite enclaves, most of which are quite small areas round villages.

The two areas of Rain Forest particularly dealt with in the present studies are the southern part ("Block 1" of the Nigerian Forestry Department's enumeration) of the Shasha Forest Reserve in Ijebu Province and the neighbourhood of Nikrowa Camp in Okomu Forest Reserve, Benin Province.

The Shasha Forest Reserve was constituted in 1925. It has an area of some

¹ Ainslie's map (1926, fig. 7) includes much Mixed Deciduous and transitional Forest in the Rain Forest Zone and therefore shows it as much too broad, especially in Ondo Province.

660 sq. miles (1709 km.²). The southern part is bounded by the Shasha (or Omo) and the Oni rivers, the confluence of the two forming the southernmost point of the reserve. Farther north the Oni continues to form the eastern boundary, but the western boundary crosses the Shasha so that a large tract of land to the west of it is included. The greatest width of the reserve from east to west is at the northern end and is about 27 miles (43 km.). The length from north to south is about 40 miles (64 km.). About 4 miles below its confluence with the Shasha the Oni runs into Lekki Lagoon, a large shallow sheet of fresh water forming part of the coastal chain of lagoons referred to above. The southern point of the reserve is about 10 miles (16 km.) from the sea and is situated about on the line dividing the coastal swamps from the drier ground. At the northern end of the reserve the Rain Forest is beginning to pass into Mixed Deciduous Forest, but none of it is really typical Mixed Deciduous Forest. It therefore represents a cross-section through the whole width of the dry-land Rain Forest Zone.

In the extreme south the reserve is very low-lying with much swamp. The ground soon begins to rise gradually and becomes more and more hilly and rocky towards the north. In the southern part of the reserve the underlying crystalline rocks are covered with a great depth of soil, mostly of Tropical Red Earth type, and probably in places with Tertiary deposits as well. The southernmost granite outcrop seen by us was near Osho's Camp, about 8 miles (13 km.) north of the southern boundary of the reserve. At Ajebandele, nearly due east of this point, igneous rocks form a large barrier across the Oni river. Northwards from this line outcrops become increasingly common.

The population of the reserve is estimated at 3000 and is mostly concentrated in small villages in the north-west and along the lower part of the Shasha and Oni. There are a few very small farming enclaves between the main rivers. The whole reserve is traversed by paths, and even the most remote parts of it are visited from time to time by hunters and fishermen from the surrounding villages.

The camp of the Cambridge Expedition was situated on the Olomitutu stream about $\frac{1}{2}$ mile (0.8 km.) west of the Oni and about 8 miles (13 km.) north-east of the Oni-Shasha junction. The neighbouring country consisted of hills, the highest perhaps 200 ft. (61 m.) high, with swampy valleys between. There were several large farming enclaves in the neighbourhood. The village of Akilla was about 5 miles (8 km.) to the south-west.

The Okomu Forest Reserve lies in the south-western corner of Benin Province between the Siluko and Osse rivers. It is wholly within the Rain Forest Zone and seems to consist mainly of low ridges and plateaux of Benin Sands, a reddish brown stoneless sand of Tertiary age. The only part visited by the Cambridge Expedition was that immediately surrounding Nikrowa (also written Nikorowa, Onikrowa, etc.) Camp, a lumber camp worked by the United Africa Company, situated on a small river in the south-east of the reserve,

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about 2 miles (3 km.) west of the Osse. This place was about 33 miles (53 km.) from the sea and some 74 miles (119 km.) south-west of Akilla. The neighbouring country consisted entirely of high forest on a level plateau raised perhaps 50 ft. (15 m.) above the river. The water of Nikrowa Creek, like that of all the rivers rising in the Benin Sands, is remarkable for its extreme clearness. Owing to the porosity of the soil there are no small forest streams in this district.

III. CLIMATE

The climate of the Rain Forest Zone in Nigeria is of the equatorial type: the temperature is high and equable and there are two maxima of rainfall in the year. One is in June and July, the other in September, but the intervening period cannot be called a dry season, for, though the rainfall is considerably less than at the maxima, it is still very heavy. For practical purposes, therefore, the year can be divided into a dry season, December, January and February, and a wet season from April to October inclusive, the remaining months being transitional. The beginning of the wet season is marked by frequent thunderstorms accompanied by violent squalls of wind and this period of the year is often called the tornado season.

The prevailing wind throughout the year is a breeze from the south or south-west, but in January and February the dry Harmattan, a northerly wind from the Sahara, which in Northern Nigeria blows throughout the dry season, at times reaches the Rain Forest Zone.

(a) RAINFALL

In the Shasha Reserve rainfall data are available for Akilla, where records have been kept by an employee of the Forestry Department since 1920.¹ Akilla is 5 miles (8 km.) from the Cambridge Expedition Camp, and its rainfall was probably typical for the southern part of the reserve in general. The mean annual total for 1921-34 was 2080 mm. (82 in.). The distribution of the rainfall through the year is shown in Table I.

The monthly distribution of rainfall at Akilla is shown also in a graphical form in Fig. 2. There are no rainfall data for the Nikrowa district, but records have been kept for over 25 years at Sapele, which lies 37 miles (60 km.) to the south-west, and at Benin, which lies 23 miles (37 km.) to the north-west: in spite of the well-known local irregularities in the distribution of rainfall in the tropics, it seems fair to assume that the mean annual total and the distribution through the year at Nikrowa will be not unlike those at these stations. At Sapele the annual total is greater than at Akilla, viz. 2605 mm. at Benin it is slightly lower, 2047 mm. (averages for 1904-13, from the *Nigeria Handbook*, 1933). The monthly means for Sapele are given in Fig. 3; the seasonal distribution

¹ We have to thank the Department for allowing us to make use of these manuscript rainfall records. We checked the monthly totals carefully and though the exposure of the rain gauge was not quite in accordance with the standard requirements the records are probably fairly reliable.

Table I. *Rainfall at Akilla, Shasha Forest Reserve, Nigeria*

	January	February	March	April	May	June
Mean monthly rainfall (mm.)	28 (± 23)	35 (± 15)	96 (± 37)	180 (± 38)	196 (± 34)	407 (± 62)
Mean no. of rainy days	1.4	2.9	7.6	9.2	12.8	18.1
	July	August	September	October	November	December
Mean monthly rainfall (mm.)	419 (± 117)	134 (± 52)	252 (± 57)	242 (± 54)	80 (± 17)	11 (± 8)
Mean no. of rainy days	16.9	12.5	18.3	16.2	7.9	1.4

The figures in brackets below the monthly means are the "fiducial values" (of Fisher) or $t \times$ the standard deviation of the mean: they represent the limits within which there is a 19:1 chance that the hypothetical "true mean" (of an infinite number of years) will fall, and are thus a measure of the variability of the rainfall from year to year. These values were kindly worked out by Dr G. C. Evans.

at Benin is very similar. The greater part of the excess of rainfall over that at Akilla is accounted for by heavier rainfall during the second (September) maximum. At both Sapele and Benin the dry season is about as long as at Akilla, and the total rainfall in the dry months is only slightly more. The rainfall figures for Akilla, Sapele and Benin are typical for rain-forest localities west of the Niger, but in the Niger delta and the south-east of the country annual totals are generally considerably higher and the dry season somewhat shorter and less intense.

(b) OTHER CLIMATIC FACTORS

Though there are no temperature data for either Akilla or Nikrowa, temperature conditions are so similar throughout the Rain Forest Zone that a very fair idea of the probable mean temperatures can be obtained from the figures published by Brooks (1920 *a*). It can be assumed that in both places the annual mean is about 25.5° C., the mean daily maximum about 31° and the mean daily minimum between 18° and 24°. Throughout the Rain Forest Zone the range of the monthly means is only about 3°; the mean daily range varies in different places from about twice to about four times this figure.

According to Brooks (1920 *b*) the mean relative humidity at 9 a.m. at stations in the Rain Forest Zone varies from about 80 to 87 %. In some localities the mean for the dry season months is as low as 78 %. These figures, however, are of little value, as the minimum values reached during the middle of the day are probably much more significant than those at 9 a.m.

No data are available on wind velocity, but general observation suggests that during most of the year, as is usual in the equatorial region, wind velocities are low. During the tornado season, locally and for periods of a few minutes, winds of high velocity are common: these tornadoes must have a considerable effect in shortening the life of old or insecurely rooted trees.

The impression given by the above data is that in south-western Nigeria we are dealing with a rain-forest climax very close to its climatic limit and it will

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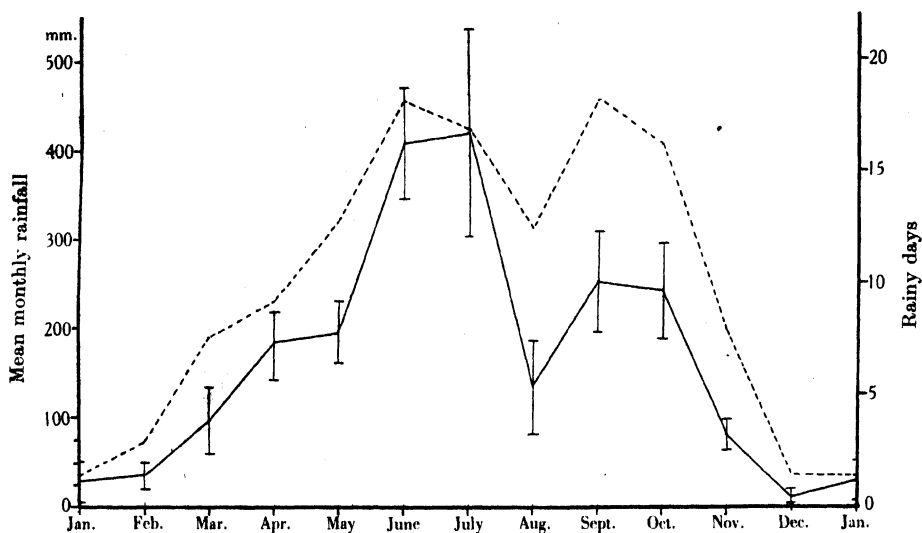


FIG. 2. Rainfall of Akilla, Shasha Forest Reserve, from observations made by an employee of the Nigerian Forestry Department.

The continuous line indicates the mean monthly rainfall. The ends of the vertical lines show the "fiducial values" (see text, p. 7). The broken line indicates the number of rainy days.

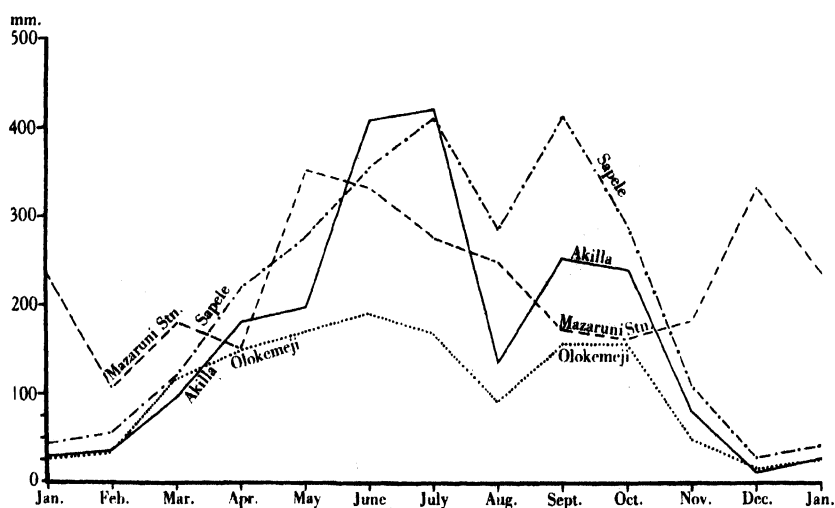


FIG. 3. Mean monthly rainfall at Akilla compared with that at Sapele (Rain Forest, Southern Nigeria), Mazaruni Station (Rain Forest, British Guiana), and Olokemeji (Mixed Deciduous Forest, Southern Nigeria).

be interesting to compare, for instance, the rainfall figures for Akilla with those for a typical locality in the British Guiana Rain Forest (Davis & Richards, 1933, pp. 355-7). In the latter the annual total is higher (2670 mm., as compared with 2080 mm.) and, what is more significant, the distribution through the year is much more even (Fig. 3). In the Guiana locality no month has a mean of less than 107 mm., while at Akilla, no less than five consecutive months have a rainfall of under 100 mm. and one of them has only 11 mm. It may be noted also that in the Guiana locality the rainfall during the wet seasons is not so excessive as at Akilla (wettest month 350 mm., as compared with 419 mm. at the latter). Even at Nikrowa, where the total rainfall is probably greater than at Akilla and the dry season a little less rigorous, conditions are certainly still much further from the optimum for Rain Forest development than in Guiana.

It will also be of interest to compare the rainfall regime of localities in the Rain Forest Zone of south-western Nigeria with some in the Mixed Deciduous Forest Zone:

Table II. *Rainfall in the Rain Forest and Mixed Deciduous Forest Zones, south-western Nigeria*

	Rain Forest Zone					Mixed Deciduous Forest Zone				
	Sapele	Akilla	Benin	Lagos	Epe	Ondo	Ibadan	Oloke-meji	Abeokuta	Oyo
Mean annual rainfall (mm.)	2604	2080	2047	1840	1679	1557	1315	1310	1262	1231
No. of months with rainfall less than 100 mm.	3	5	5	6	6	4	6	5	5	6
No. of months with rainfall less than 50 mm.	2	3	3	3	5	3	4	4	4	3
Mean rainfall for December, January and February (mm.)	127	74	98	99	63	81	62	77	84	63

Data for Epe from Brooks (1916), for Akilla from MS. records of the Nigerian Forestry Department, for the remaining stations from the *Nigeria Handbook* (1933).

These data show that the boundary between the Mixed Deciduous Forest and the Rain Forest corresponds approximately, in this area, with the isohyet of 1600 mm.¹ As during the wet season the rainfall must be more than adequate for the needs of the vegetation everywhere in both zones, we might have expected that the boundary would be determined by the length of the dry season or the total rainfall during the dry months. The figures in Table II, however, do not support such a view, and it is therefore possible that the boundary depends primarily not on the rainfall itself, but on some factor correlated with it, such as the distance inland reached by moist air from the sea during the dry

¹ Aubréville (1936, p. 8) gives 1600 mm. as the lower limit of rainfall for evergreen Rain Forest on the Ivory Coast.

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season. The figures for Epe confirm this suggestion. This locality, though it has a longer dry season and less rain during the dry months than some Mixed Deciduous localities, lies in the Rain Forest Zone. The reason is almost certainly its nearness to the sea and a large lagoon. The data for the distribution of relative humidity, for the reason already mentioned, throw little light on this question. Mean maximum temperatures are rather higher in the Mixed Deciduous Forest than in the Rain Forest Zone, but the annual mean is about the same in both.

The difference of climate determining the two types of forest must in any case be narrow, so local conditions of soil and topography will probably be sufficient to tilt the balance where the climatic conditions are near the critical point.

The temperature and humidity conditions within the Rain Forest will be discussed in detail by Dr G. C. Evans in a later contribution to these "Studies".

(c) SEASONAL CHANGES IN THE VEGETATION

Compared with Rain Forest in general our area has an unusually well-marked periodicity of climate, and this might be expected to show itself in the seasonal rhythms of the vegetation.

The Cambridge Expedition was in Nigeria from January to the end of May 1935, that is from about half-way through the dry season till well into the wet season. The tornado season set in at the end of March. In the primary forest, except for the large number of branches blown down from the trees and the great increase in the number of species in flower, little change was noticeable. In the secondary forest and farm land, on the other hand, there was a general outburst of vegetative growth as well as of flowering. In the swamps the large aroid, *Cyrtosperma senegalense* (Schott) Engl., began to put out new leaves with astonishing vigour.

So far as it is possible to generalize from the scanty data available, the state of affairs in the primary forest seems to be that though flowers can be found at all times of year, there is evidently a maximum flowering period at the beginning of the wet season: possibly there is another at its close. Undergrowth species as well as tall trees seem to have fairly definite flowering seasons; for instance, species of *Rinorea*, which are some of the commonest members of the shrub layer, came into flower everywhere in the southern Shasha Reserve at the beginning of February: by March they were all in seed and they did not flower again during our stay. In British Guiana (Davis & Richards, 1933, p. 359) and Sarawak (Richards, 1936, p. 8) undergrowth species did not appear to have definite flowering seasons, but could be found in flower at any time.

With regard to leaf fall, the trees of the southern Shasha Reserve can be grouped into (a) those which are evergreen in the usual sense, i.e. shed their leaves fairly steadily throughout the year or at least over a long period,

(b) those which lose all their leaves at once, but produce new foliage simultaneously, so that they are never bare, (c) deciduous species which are bare for a more or less long period.

Trees of class (c) are rare in the primary Rain Forest, but frequent in secondary forest and clearings. The commonest are *Albizzia gummifera* (Gmel.) Sm. (93), *Bombax* sp. cf. *flammeum* Ulbrich (3039), *Ceiba pentandra* Gaertn. and *Terminalia superba* Engl. & Diels (3040). The bare period did not coincide by any means exactly with the dry season, some species becoming leafy before the end of the dry season, others not till some time after it. There was also much individual variation in any one species.

In the primary forest the majority of the trees belong to class (a), but class (b) is well represented, e.g. *Casearia bridelioides* Mildbr. ex Hutch. & Dalz. (69, 3046, etc.). Many species, e.g. *Lophira procera* A. Chev., vary between class (a) and class (b).

The introduced teak, *Tectona grandis* L.f., which in tropical localities with a less marked dry season (such as Singapore) becomes evergreen, is deciduous in the plantations at Akilla, the trees remaining bare for some weeks.

In connexion with seasonal changes it is interesting to note that in the primary forest there were at least two species of geophytes, a life form generally sparingly represented or quite absent in the Tropical Rain Forest. One of these, *Cyanastrum cordifolium* Oliv. (3083, 3338), is a small monocotyledonous herb which dies down completely in the dry season. The tuber is about 5 cm. below the surface of the soil and the young shoots spring up at the beginning of April. The other geophyte is *Icacina trichantha* Oliv. (3142, etc.), a weak shrub, 1-2 m. high, frequent in the undergrowth. The large woody tuber is found at a depth of 10-15 cm. This plant does not die down completely in the dry season, but at the beginning of the rains new shoots come up and rapidly unfold their leaves.

In the secondary forest in addition to these two there were several other species with bulbs, corms or tubers, e.g. *Anchomanes difformis* (Bl.) Engl. (43), *Crinum Jagus* (Thompson) Dandy (17, 42), *Dioscorea* spp. and *Haemanthus cinnabarinus* Decne. (3079, 3417). The second of these is also common in openings of the primary forest, swampy places and river banks.

Generally speaking, it seems that seasonal periodicity is somewhat more marked in the primary vegetation of our area than in that of British Guiana, but in spite of the very pronounced dry season deciduous trees are no more common than they are there.

IV. EXPLOITATION OF THE FOREST

The Rain Forest of south-western Nigeria, even where it has not been completely destroyed, has suffered enormous damage, on the one hand from native farmers practising shifting cultivation and on the other from the commercial

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exploitation of the timber. The area of forest in an even approximately primary condition is already very small, and, since timber exploitation, though not farming, continues even in the so-called forest reserves, it is still rapidly diminishing. From the botanical point of view, if from no other, it is much to be regretted that no forest areas have been completely protected against human interference.

In the southern part of the Shasha Reserve there are considerable areas of active and abandoned farm land. In the last few years, however, farming enclaves have been demarcated round all the villages and no farming is now carried on outside them. Timber working was probably started about 1900 or 1901. It continued on a moderate scale up to 1914, and the species exploited were chiefly the Meliaceae (mahoganies), *Khaya ivorensis* A. Chev., *Lovoa Klaineana* Pierre ex Sprague, and to a lesser extent, *Entandrophragma* spp. From 1915 to 1919, owing to wartime demands, exploitation was much intensified and a great many other species were also felled. In recent years timber working has been much less active as most of the best trees have been removed, but hauling roads and other signs of exploitation are met with everywhere, even 6 miles (10 km.) from the Oni.

Our second area, the Nikrowa district, has been less farmed than the Shasha Reserve, but timber working has been carried on for nearly as long. The number of valuable trees was, however, originally much greater, and exploitation is being carried on intensively at the present time. A light railway runs for some miles into the forest from the Nikrowa creek, and hauling roads radiate in all directions. The species worked are *Triplochiton scleroxylon* K. Schum. and *Sarcocephalus Diderrichii* De Wild., and the mahoganies, *Khaya ivorensis* A. Chev., *Entandrophragma cylindricum* Sprague, *E. macrophyllum* A. Chev., and *Guarea Thompsonii* Sprague & Hutch.

The effects of farming and timber working on the forest are very different. In farming all the original vegetation is destroyed, except for a few large trees which are left for shade, for possible use as timber, for superstitious reasons or because their felling would be too laborious. When after a number of years the land is exhausted, it is abandoned and a secondary succession starts, the course of which will be the subject of a subsequent paper by Mr R. Ross. In timber working, on the other hand, destruction is much less complete and the vegetation, if left to itself, would no doubt return quite quickly to its original condition. As the valuable timber species are always found scattered through a mixed community, clear-felling is never practised, but the large trees in falling injure a considerable number of their smaller neighbours and large quantities of small trunks are needed to make rollers for the hauling roads, so far more trees are felled than are actually used. The type of forest which remains in areas which have been closely worked for timber has a characteristic aspect, different from that of both the primary forest and the true secondary forest: it may perhaps be called depleted forest. In floristic composition it comes nearer

to primary forest, but in addition to most of the species found in primary forest, most of those of secondary forest are also present in abundance. Its structure is exceedingly irregular: there is no continuous undergrowth stratum of trees and large "holes", filled with impenetrable tangles of shrubs and creepers, are very common. The depleted forest is, in fact, an irregular patch-work of fragments of primary and secondary forest, and the general impression it gives is of a chaotic mass of vegetation.

The greater part of the forest on dry land in both the southern Shasha Reserve and the Nikrowa area is secondary or heavily depleted; in each, however, there were small patches of forest a few hectares in extent which were believed to be primary or at least to approximate closely to primary forest in structure and floristic composition. The natives do not make a sharp distinction between primary and secondary forest: young secondary forest is spoken of as "low bush", but the term "high bush" includes any forest containing a fair number of large trees, whether virgin, depleted or old secondary. It was therefore necessary to rely on general considerations to decide what was and what was not primary forest. The patches of dry-land forest described in this paper are believed to be approximately primary for the following reasons:

(1) The absence of cut stumps, relict cultivated plants (e.g. bananas, oil palms) or other signs of interference.

(2) The abundance of large trees and also of trees of sizes intermediate between these and the smaller ones.

(3) The scarcity of species common in forest known to be secondary, e.g. *Alchornea cordifolia* (Schum.) Muell. Arg., *Fagara macrophylla* (Oliv.) Engl. (3433), *Macaranga Barteri* Muell. Arg. (3246), *Musanga Smithii* R. Br., *Trema guineense* (Schum.) Ficalho.

(4) The abundance of species which are rare in forest known to be secondary, e.g. *Diospyros insculpta* Hutch. & Dalz. (90, 155, etc.), *Casearia brideioides* Mildbr. ex Hutch. & Dalz. (69, 3046, etc.).

(5) The undergrowth not excessively dense and is often very sparse (Pl. I, phot. 1).

(6) Lianes only moderately abundant.

(7) A general resemblance in aspect to primary forest in Malaya, Borneo and British Guiana.

With regard to the number of large trees on the sample plots of Mixed Forest, see pp. 36-7.

Even in these patches of primary forest small "holes" were commoner than in primary forest in either Borneo or Guiana: this, however, may be due to tornadoes, which seem to be particularly common and violent in Nigeria and which often blow down large trees which would otherwise have rotted away gradually.

The survival of these patches of primary forest is usually due either to their being situated in places from which it is difficult to extract timber (e.g. tongues

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of dry land surrounded by swamp) or to a lack of commercially valuable trees. In the latter case it is possible that they do not form a completely fair sample of the composition of original forest: this, however, is not likely to affect their structure, which is probably typical.

The swamp forest is naturally much less interfered with than that on dry land. Commercially valuable trees are less common in it and few natives visit it. It was always considered to be primary when there were no obvious signs of timber working.

Larger stretches of primary forest than those in our two areas might possibly have been found farther north in the Shasha and Okomu Reserves, but such forest would probably have already been transitional to Mixed Deciduous Forest and not typical Rain Forest. Extensive areas of primary Rain Forest no longer exist in Nigeria, except perhaps in the Oban Hills and the Cameroons region in the south-east.

Indeed, it is not usually realized how little primary forest remains at the present time in West Africa generally. Many writers on the forest vegetation have made no attempt to define the criteria by which primary forest can be recognized, nor have they reckoned seriously with the possibility that by far the greater part of the vegetation they are dealing with is secondary or at least heavily depleted and much modified.

V. TYPES OF VEGETATION

The primary forest habitats of south-western Nigeria fall naturally into two main divisions, (i) the dry land not subject to flooding, and (ii) the swamps which are flooded for a longer or shorter period every year. On the dry land in the Shasha Forest Reserve only one type of primary forest could be recognized—the Mixed Rain Forest. The structure of this seemed to be similar wherever it occurred, though the floristic composition varied considerably from place to place. The primary forest on dry land at Nikrowa, though it differed somewhat from that in the Shasha Reserve, was of the same general type and can therefore be considered as another facies of the Mixed Rain Forest, which is the climatic climax of the whole zone. Both in the Shasha Reserve and at Nikrowa land liable to flooding is occupied by various types of vegetation, of which the highest is the Fresh-water Swamp Forest. This is here regarded as an edaphic climax.

(1) MIXED RAIN FOREST (CLIMATIC CLIMAX)

(a) *Soil*

The soils of the primary Mixed Rain Forest are of the Tropical Red Earth, or, less frequently, of the Tropical Yellow Earth, type. In texture they show some variation, but there was not nearly as wide a range of soils as, for instance, at Moraballi Creek, British Guiana (Davis & Richards, 1934). In the southern part of the Shasha Reserve the soil is everywhere clayey or

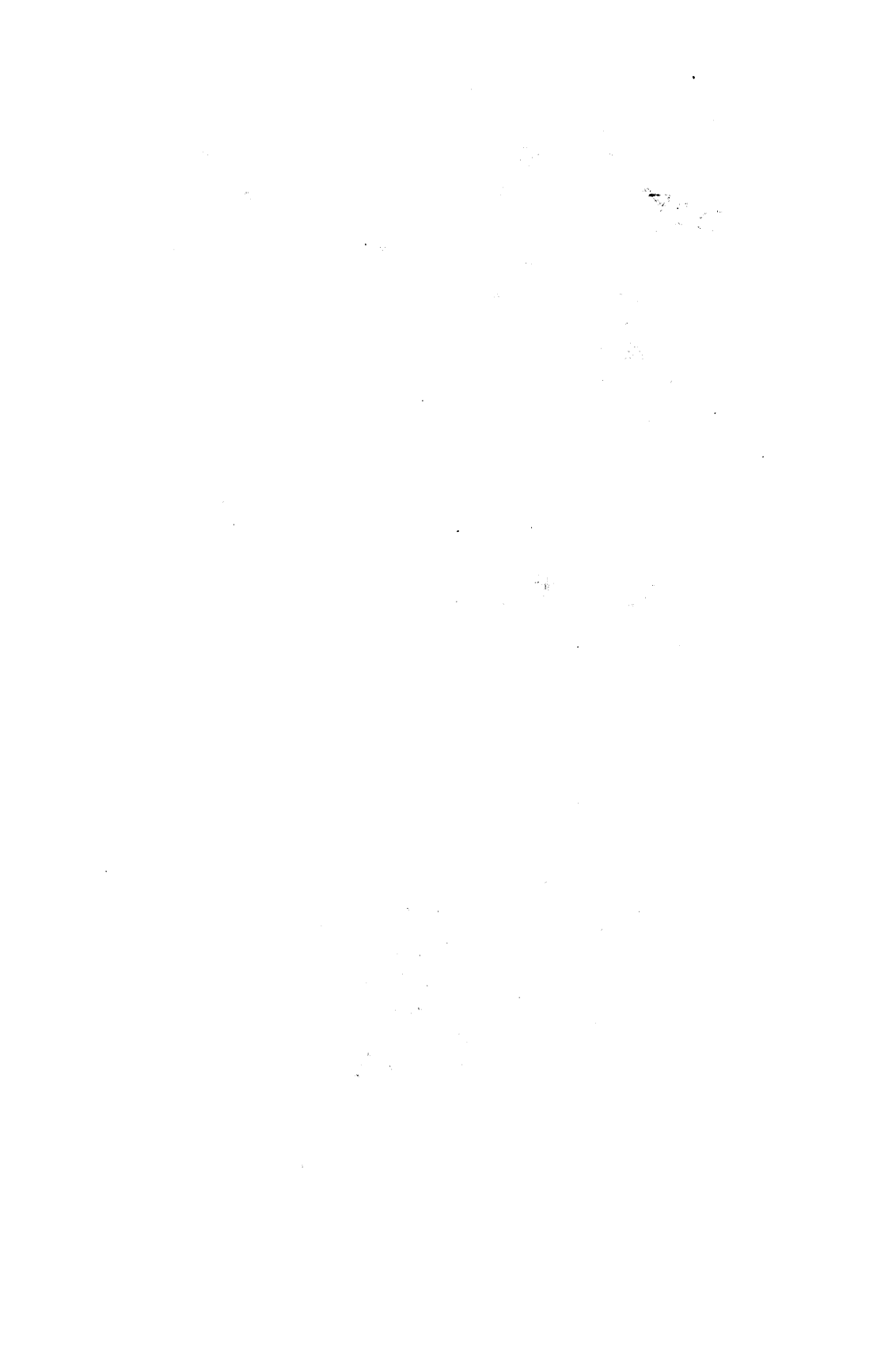


Phot. 1. Primary Mixed Rain Forest, Sample Plot 3, near Nikrowa Camp, Okomu Forest Reserve. The large tree is Ijebu (*Entandrophragma macrophyllum* A. Chev.: note the surface roots characteristic of the species.



Phot. 2. Large climbers and a "Strangling" Fig (*Ficus* sp. on a large Erun tree) (*Erythrophloeum micranthum* Harms), primary Mixed Rain Forest, near the Cambridge Expedition's Camp, Shasha Forest Reserve.

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loamy, but the soil in the primary forest near Nikrowa (derived from the Benin Sands) is much lighter and may be described as a brown sand.

Soil profiles in the primary Mixed Forest were studied by Mr W. J. F. Campbell and at four typical sites soil samples and monoliths were collected. The following are the descriptions and analyses of these profiles; further details will be found in an unpublished thesis by Mr Campbell (1936).

Profile 1 (A 27¹). Primary Mixed Rain Forest, Sample Plot 1 (cf. p. 35), about 8 km. north of Akilla, Shasha Forest Reserve.

Description:

Horizon I. 0-5 in. (0-13 cm.). Light brown, with some bleached sand grains in the extreme top. Little or no leaf litter. Sandy loam. Granular. Porous. Moist and well drained right through. Thick root mat in the top few inches.

Horizon II. 5-15 in. (13-38 cm.). Reddish yellow, with some iron mottlings. No visible humus. Medium loam. Granular. Slightly cemented. Roots frequent and carbon deposits in old root channels. Quartzose fragments. Some accumulation of iron at 12 in. (30 cm.).

Horizon III. 15 in. (38 cm.) downward. Reddish, colour increasing in intensity with depth. No visible humus. Sandy loam. Granular. More cemented than horizon above. Some quartzose fragments. Roots frequent.

Type: Tropical Red Earth.

Analysis:

Horizon	I	II	III
Loss on ignition	3.7	2.4	2.6
Mechanical analysis (as percentage of mineral matter):						
Coarse sand				31.2	24.5	29.7
Fine sand				42.8	30.7	38.0
Silt				8.1	9.0	12.2
Clay				16.8	34.8	19.7
Clay analysis:						
SiO ₂ (%)				29.2	36.5	38.5
Al ₂ O ₃ (%)				25.5	37.6	38.4
Fe ₂ O ₃ (%)				5.8	6.9	7.2
SiO ₂ Al ₂ O ₃				1.9	1.6	1.7
SiO ₂ Al ₂ O ₃ + Fe ₂ O ₃				1.6	1.5	1.5
Organic analysis:						
Carbon (%)				2.9	0.63	0.47
Nitrogen (%)				0.03	0.07	0.05
C/N				17.2	15.2	16.1
pH				3.5	4.0	3.5

¹ Numbering of the profiles as given by Campbell (1936).

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Profile 2 (A 28). Patch of primary Mixed Rain Forest near the Cambridge Expedition Camp, Shasha Forest Reserve.

Description:

Horizon I. 0-3 in. (0-8 cm.). Dark brown, with bleached sand grains. Some leaf litter and mull. Sandy loam. Granular. Porous and loose. Thick root mat in the top few inches. Excessive drainage. Clearly delimited below.

Horizon II. 3-12 in. (8-30 cm.). Light brown. Slight traces of intimate humus. Sandy loam. Nutty structure. Traces of cementing in bottom inches. A band of iron concretions occurs at 10 in. (25 cm.). Merging into III.

Horizon III. 12-40 in. (30-102 cm.). Red-yellow. No visible humus. Medium loam. Nutty structure. Increasing cementation with depth. Frequent roots. Merging into IV.

Horizon IV. 40 in. (102 cm.), downwards. Dark red with yellow mottlings. No visible humus. Medium loam. Nutty structure. Compact. Mottlings and concretions of iron. Increasing compactness with depth. Frequent roots.

Type: Tropical Red Earth.

Analysis:

Horizon	I	II	III	IV
Loss on ignition	4.0	3.5	5.9	5.9
Mechanical analysis (as percentage of mineral matter):				
Coarse sand	32.7	20.8	23.4	21.7
Fine sand	38.0	36.2	27.0	32.8
Silt	14.1	17.2	18.0	20.1
Clay	24.2	25.8	20.1	23.0
Clay analysis:				
SiO ₂ (%)	24.6	36.4	35.8	36.0
Al ₂ O ₃ (%)	31.3	36.2	35.0	45.2
Fe ₂ O ₃ (%)	5.3	8.2	7.6	7.6
SiO ₂ Al ₂ O ₃	1.3	1.7	1.7	1.4
SiO ₂ Al ₂ O ₃ + Fe ₂ O ₃	1.2	1.6	1.5	1.3
Organic analysis:				
Carbon (%)	2.0	0.85	0.2	0.3
Nitrogen (%)	0.28	0.07	0.02	0.025
C/N	18.2	20.3	17.6	19.8
pH	3.0	3.5	4.0	4.5

Profile 3 (A 32). Slightly depleted Mixed Rain Forest, Sample Plot 2 (cf. p. 35), near Eluju village, about 5 km. north of Akilla, Shasha Forest Reserve.

Description:

Horizon I. 0-4 in. (0-10 cm.). Light brown. Little humus visible. Sandy loam. Granular. Porous and loose. Few bleached sand grains on surface. Merging into II.

Horizon II. 4-40 in. (10-102 cm.). Yellow-brown. Traces of intimate humus. Light loam. Granular. Porous and slight traces of cementation. Very few roots. Clearly delimited below.

Horizon III. 40 in. (102 cm.), downwards. Yellow. No humus. Light loam. Nutty. Less cemented than the horizon above. Iron concretions in quantity.

Type: Tropical Yellow Earth.

Analysis:

Horizon	I	II
Loss on ignition	3.2	4.0
Mechanical analysis (as percentage of mineral matter):					
Coarse sand				32.4	38.1
Fine sand				37.1	30.8
Silt				11.4	14.3
Clay				18.1	15.2
Clay analysis:					
SiO ₂ (%)				32.7	39.1
Al ₂ O ₃ (%)				31.27	39.8
Fe ₂ O ₃ (%)				5.93	6.88
SiO ₂				1.8	1.7
Al ₂ O ₃					
SiO ₂				1.6	1.5
Al ₂ O ₃ + Fe ₂ O ₃					
Organic analysis:					
Carbon (%)				1.6	0.58
Nitrogen (%)				0.1	0.05
C/N				17.2	20.2
pH				5.6	5.0

Profile 4 (A 37). Primary Mixed Rain Forest, Sample Plot 3 (cf. p. 35), about 6 km. north of Nikrowa Camp, Okomu Forest Reserve.

Description:

Horizon I. 0-12 in. (0-30 cm.). Brown. Some humus present at top, but decreases rapidly with depth. Sandy loam. Crumb structure. Porous and loose. Slight cementation with depth. Very little leaf litter. Small roots frequent. Merging into II.

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Horizon II. 12 in. (30 cm.), downwards. Deep red. No humus visible. Light loam. Crumb structure. Porous, though cemented. Colour tends to deepen with depth.

Type: Tropical Red Earth.

Analysis:

Horizon	I	II A 12-40 in. (30-84 cm.)	II B 40 in. (84 cm.) downwards
Loss on ignition	3.0	4.7	7.1
Mechanical analysis (as percentage of mineral matter):						
Coarse sand				38.1	36.0	38.4
Fine sand				40.2	37.3	36.0
Silt				6.8	7.2	7.9
Clay				13.0	17.2	15.0
Clay analysis:						
SiO ₂ (%)				34.9	36.6	38.7
Al ₂ O ₃ (%)				37.9	36.4	42.0
Fe ₂ O ₃ (%)				7.63	8.53	8.56
SiO ₂				1.6	1.7	1.6
Al ₂ O ₃						
SiO ₂				1.4	1.5	1.4
Al ₂ O ₃ + Fe ₂ O ₃						
Organic analysis:						
Carbon (%)				3.5	2.6	0.4
Nitrogen (%)				0.03	0.03	0.005
C/N				18.2	15.1	13.7
pH				6.2	5.8	5.0

(b) *Structure*

The primary Mixed Rain Forest can be regarded as built up of the following groups of plants:

A. Autotrophic.

- (1) Plants not dependent on others for mechanical support (trees, shrubs and herbs).
- (2) Plants dependent on others for mechanical support.
 - (a) Climbers and hemi-epiphytes.
 - (b) Epiphytes (including the hemi-parasitic Loranthaceae).

B. Heterotrophic.

- (a) Saprophytes.
- (b) Parasites.

Each of these groups can be further subdivided into synusiae. The synusiae of the "independent" plants consist in the first place of layers or strata, each layer forming one synusia, except the herb stratum, which consists of more than one.

(i) *Stratification of the trees.*

The stratification of the trees was studied by means of two clear-felling plots from which profile diagrams have been drawn (Figs. 4 and 5). Both plots were situated in patches of primary forest near the Cambridge Expedition Camp in the Shasha Reserve. Clear-felling Plot I formed part of Sample Plot 2 and Clear-felling Plot II part of Sample Plot 1. A description of the sites of these plots is given below (p. 35) and their soils have been dealt with already (pp. 15-18). No clear-felling plots were made in the Nikrowa area.

Each clear-felling plot was 200×25 ft. (61×7.6 m.) and on each all trees 15 ft. (4.6 m.) high and over were felled and measured. The measurements made and the method of constructing the profile diagrams were the same as those used for the forest in Sarawak (cf. Richards, 1936, p. 10).

On Clear-felling Plot I (Fig. 4) we can recognize the following strata, from below upwards: (i) a dense story of trees about 25-50 ft. (7.6-15 m.) high. The crowns of these undergrowth trees are packed closely together and form the highest completely closed stratum or canopy in the forest. Out of the sixty-four trees under 50 ft. (15 m.) high on this plot ten are young individuals of taller species and the remainder individuals of seven species belonging to this story. As only trees over 15 ft. (4.6 m.) high are included in the diagram this story appears in the diagram to be cut off sharply below: actually, it passes insensibly into the shrub stratum.

Above the lowest story there is an irregular mass of trees of various heights, the tallest of which is 149 ft. (46 m.) high. The crowns of these trees are sometimes in contact with each other laterally, but there is no closed canopy at any level. Observation over the whole of S.P. 4 (of which C.F.P. I formed only a part) showed that this irregular mass could be considered as consisting of two not very sharply separated strata, viz. (ii) an irregular middle story of trees about 50-120 ft. (15-37 m.) high: these have small crowns, seldom more than 30 ft. (9 m.) wide and belong to a considerable number of species, and (iii) a top story of trees 120-150 ft. (37-46 m.) high. These usually have umbrella-shaped crowns, which may be over 80 ft. (25 m.) broad: their lowest leaves are about on a level with the tops of the tallest trees in the middle story. Trees of this story are scattered fairly evenly through the forest. On C.F.P. I they are represented by a single large tree of *Lophira procera* A. Chev. only, but in S.P. 2 as a whole the commonest species is *Erythrophleum micranthum* Harms (3376*, 3453*). Young individuals and seedlings of these large species, especially of the latter, are very rare: on S.P. 2 there were thirteen trees of *Erythrophleum* of 24 in. (61 cm.) diameter and over, but no smaller individuals were seen. The very poor regeneration of the larger trees in the African Rain Forest has been previously commented upon by Mildbraed (1930b, pp. 54-5).

A striking feature of C.F.P. I is the complete break in the middle story

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under the large *Lophira*: between its crown and the third story there is an empty space.

On C.F.P. II (Fig. 5) the stratification is similar except that the tallest tree is only 106 ft. (33 m.) high. Much taller trees were, however, present in the adjacent forest. The clear-felling plots are so small that they will not necessarily contain even one individual belonging to the first story. Very large trees were, however, certainly scarcer on S.P. 1 than on S.P. 4, and on C.F.P. II even the middle story is not represented by many individuals. The growth here is in fact altogether poorer than on C.F.P. I. The reason for this is perhaps the harder, more cemented soil (cf. soil profiles 1 and 3, pp. 15 and 17), but this piece of forest may have been somewhat depleted in the past. Out of the sixty-five trees under 50 ft. (15 m.) high on C.F.P. II, five are young individuals of taller species and the remainder individuals of six true third-story species.

Further evidence as to the stratification and general structure of the Mixed Forest in the Shasha Reserve was obtained by climbing a tree in a small patch of primary forest close to the Cambridge Expedition's camp. A rope ladder was fixed to this tree up to 78 ft. (24 m.) (primarily for making meteorological observations), so the surrounding forest could be examined at leisure. The photograph taken from this ladder, at a height of 78 ft. (24 m.), is reproduced in Pl. II, phot. 3.

The views from this tree confirmed very strikingly the general conception of the forest structure given by the two clear-felling plots. Up to 30–40 ft. (9–12 m.) there is a dense mass of third-story trees whose crowns form a closed canopy bound together by climbers into a coherent undulating sheet of foliage. The larger trees rise above this to various heights, the tallest to about 150 ft. (46 m.), but do not form a closed canopy at any higher level. Above about 35 ft. (11 m.) it was possible to see for some distance on all sides. When climbing the ladder, after passing the canopy of undergrowth trees, one seemed to emerge into full daylight.

The stratification of the Mixed Forest at Nikrowa showed no important differences from that on the two clear-felling plots, as far as could be discovered. The abundance of trees of enormous height and diameter is the outstanding feature of even the depleted forest of this area, and the remaining primary forest must be some of the finest in West Africa. The tallest tree actually measured by us was a *Guarea Thompsonii* Sprague & Hutch.(?) of 150 ft. (46 m.), but estimates indicated that trees of 150–200 ft. (46–62 m.) were common and trees over 200 ft. probably not rare.

On S.P. 3 there seemed to be a dense canopy at about 45 ft. (14 m.) formed chiefly by Itako pupa, *Strombosia retivenia* S. Moore (3294*) (cf. Table VIII): as in the Shasha Forest, there did not seem to be any canopy properly so-called at a higher level. Our exploration of the district was not sufficiently thorough to decide whether this remarkably even undergrowth stratum of *Strombosia* was a purely local feature or whether it was widespread in the Okomu Reserve.

All the evidence thus gives a fairly consistent picture of the stratification of the trees in the Mixed Rain Forest of our area. Before trying to summarize it, however, it should be pointed out that any brief description of the stratification of a rain forest is apt to give the impression of something more definite than what actually exists. The rain forest is not a chaotic mass of trees, but its structure is something so ill-defined as to be extremely difficult to describe in a few words.

Bearing this in mind, we can give the following general description of the stratification: There are three strata, the *first* or top 120–150 ft. (37–46 m.) high, consisting of relatively few species, with wide-spreading crowns, not in lateral contact with each other, the *second* or middle 50–120 ft. (15–37 m.) high, consisting of a great variety of species with small crowns, occasionally in lateral contact with each other, and a *third* or lowest stratum of trees up to 50 ft. (15 m.) high: this consists chiefly of a rather limited number of true third-story species: young individuals of species belonging to the first or second strata form less than 20 % of the total number of individuals. Exceptional individuals of species normally belonging to the third stratum may reach a height of about 70 ft. (21 m.), thus forming part of the second stratum. The crowns form a closed canopy bound together by climbers.

Once a tree has emerged from the third story, the height to which it grows is perhaps determined more by its own specific height-growth potentialities than by the competition of its neighbours. The distinction between the first and second stories is therefore, as it were, “accidental”, depending on the particular assortment of species present and the relative abundance of each.

The trees of each stratum have characteristic features. Typical *first-story species*, e.g. *Azelia bipindensis* Harms (25), *Erythrophleum micranthum* Harms (3376, 3453), *Lophira procera* A. Chev., and various Meliaceae, have more or less umbrella-shaped crowns, sometimes 25 m. or more wide, supported by a candelabra-like system of branches in which the main axis is rarely well marked above the first fork. The trunks are often buttressed. The leaves tend to be small and have a short acumen or none at all. *Second-story species*, e.g. *Berlinia auriculata* Bth. (3158, 3408, 3487), *Diospyros confertiflora* Gürke (3443, etc.), *Pausinystalia* spp., *Strombosia pustulata* Oliv. (3428, 3444), and *Xylopia Quintasii* Engl. & Diels (68, 3159, etc.), usually have small, rounded crowns, under 10 m. wide; the main axis is generally distinct nearly to the top. The trunks are often buttressed. The leaves tend to be larger than those of the first-story trees and usually have an acumen about 8 mm. long. Species of the *third story*, e.g. *Rinorea* sp. cf. *oblongifolia* (C. H. Wright) Marquand (242, 3156), *Casearia* n.sp. (3081, 3157, 3191), *Diospyros insculpta* Hutch. & Dalz. (90, 155, etc.), and various Apocynaceae, often have small conical crowns with numerous nearly horizontal branches beginning low down the trunk; sometimes when old the crowns become surprisingly wide and heavy, e.g. in *Diospyros insculpta* and *Picralima umbellata* (Stapf) Stapf (8, 142, etc.). The trunks are slender and

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never appreciably buttressed. The average size of the leaves is greater than in the two previous stories: the leaves almost always have a long fine acumen (average length about 12 mm.). The only cauliflorous tree is *Diospyros confertiflora* Gürke (3443, etc.) (second story), and that is not constantly so.

No palms seem to occur naturally in primary Mixed Rain Forest, except an occasional *Raphia* sp. near the edges of swamps. Oil palms, *Elaeis guineensis* Jacq., planted or self-sown, are sometimes met with in the forest, but probably never where it is undisturbed. One monocotyledonous tree, *Dracaena Mannii* Bak. (3149), was occasional in depleted and secondary forest in the Shasha Reserve and at Nikrowa: it was never actually observed in primary forest, but probably occurs there in openings. It attains a height of about 100 ft. (31 m.), and a specimen close to S.P. 1 (Shasha Reserve) had a girth of 22 ft. (6.8 m.).

Few data are available as to the extreme heights reached by trees in our area. The tallest tree actually measured by us was a *Terminalia superba* Engl. & Diels (3040*) 153 ft. (47.1 m.) high, but, as mentioned above, trees over 200 ft. (62 m.) high are undoubtedly not rare, at any rate in the Okomu Reserve. Kennedy (1936) states that several Nigerian Rain Forest species attain 200 ft. The tallest tree so far definitely measured in Nigeria is an *Entandrophragma cylindricum* Sprague with a bole length of 154 ft. (47.4 m.): the total height was not noted (*Annual Report*, 1930, p. 25). These figures are of the same order as those for other parts of the African Rain Forest. Chipp (1927, p. 19) speaks of trees 200 ft. high in the Gold Coast, but gives no actual measurements. In the Cameroons Mildbraed (1922, p. 105) measured a tree of *Iringia glaucescens* Engl. of 56 m., which he says stood as "*par inter pares*". Jentsch (1911, p. 23) records a *Mimusops Djave* Engl. of 68 m. in the same region.

The description of the stratification here given agrees well on the whole with the scanty data for other parts of Africa. According to Aubréville (1933, p. 2) the Rain Forest of the Ivory Coast consists of a dense mass of vegetation 20–30 m. high dominated by giant trees here and there: its aspect somewhat recalls a coppice-with-standards (*taillis sous futaie*). Judging from this statement, the first and second stories in that region must be even less dense than in our area, either owing to depletion or some natural cause. In the Gaboon Chevalier (1917, pp. 354–5) distinguishes three stories of trees, 10–20, 25–35 and 40–70 m.

Though, as has been pointed out, the stratification of the trees in the Nigerian forest is very indefinite, the author cannot accept the extreme view of Mildbraed (1922, pp. 103–4), who claims that no real stratification is recognizable in the African Rain Forest. The incorrectness of this view is sufficiently proved by Figs. 4 and 5.

The stratification in the Mixed Rain Forest of Nigeria may be compared with that in the corresponding types of forest in British Guiana (Davis & Richards, 1933, pp. 362–71, Fig. 6) and Sarawak (Richards, 1936, pp. 10–13, Figs. 2 and 3).

The trees in the Guiana forest were regarded as forming only two strata, "an irregular canopy of about 24 m. average height and undergrowth trees up to about 14 m. high. Above the former many trees of up to 42 m. stand out incompletely, while here and there are exceptionally tall ['outstanding'] trees, which have their whole crown clear of their neighbours" (Davis & Richards, 1933, pp. 383-4). In Nigeria, as has been shown, we have a similar undergrowth stratum; though it consists mainly of individuals of true undergrowth species, while in Guiana about half the individuals are of species belonging to the higher stratum. The taller trees do not form a closed canopy and are regarded as forming two strata. The absence of a closed canopy above the undergrowth stratum probably represents a structural difference of some importance. If, however, Figs. 4 and 5 are compared with the similar diagram for the Guiana forest (Davis & Richards, 1933, Fig. 6) it will be clear that the fact that the taller trees are in one case considered to form two strata and in the other only one irregular stratum, is a difference in the terms of description rather than in the structure itself. The first story, in Nigeria, of trees from 37 to 46 m. corresponds to the trees up to 42 m. "which stand out incompletely from the canopy" and to the "outstanding trees". The second story in Nigeria corresponds to the "lower trees of the canopy" in Guiana, but differs in being less dense and not usually much bound together by lianes. The height of the tallest trees is probably greater in Nigeria than in Guiana, or at least trees of great height are commoner.

The Mixed Dipterocarp Forest at Mt Dulit, Sarawak, was regarded as forming three strata, average height of which is about 34, 18 and 8 m. respectively. From this it might seem that the structure differs less from that of the Nigerian forest than the Guiana forest, but the opposite is true. The first story in Sarawak is clearly marked off from the second by a definite gap, chiefly because it consists almost entirely of Dipterocarpaceae which are mostly considerably taller than the miscellaneous species which form the second story. The second story is dense and forms a closed canopy: it is only very vaguely delimited from the third story. It was estimated that more than half the latter consisted of young individuals of first- or second-story species.

If generalization is possible then, we can say that the Nigerian Forest shows a fairly close general resemblance in stratification to the Mixed Forest of Guiana and Sarawak, but differs in (a) the greater openness of the two upper strata, which results in the undergrowth stratum forming the highest closed canopy, (b) the much smaller proportion of young trees in the undergrowth stratum. (a) and (b) are doubtless closely connected, and are dependent on the poor regeneration of the taller species.

(ii) *Shrub and herb strata.*

Below the lowest tree stratum a layer of shrubs can be recognized, and below this again a layer of herbs which do not usually exceed 1 m. in height.

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The majority of the individuals in the shrub layer are young trees belonging to the undergrowth tree and higher strata. This is the reason for the fact already mentioned that there is no discontinuity between this stratum and the one above it.

The density of the shrub layer varies greatly, but as far as it was possible to judge from the limited areas of primary forest available, in undisturbed forest it is always possible to walk about without cutting a path and to see for some metres ahead (Pl. I, phot. 1). Any kind of thinning of the overlying strata causes the shrub layer to become very dense. In secondary and depleted forest and in natural or artificial openings in primary forest the undergrowth is characteristically impenetrable and makes progress slow except on well-marked paths. Locally in primary forest the shrub layer may be almost wanting.

The true shrubs are few in species as well as in individuals. Some of them, e.g. *Rinorea* spp., have a fairly typical "shrubby" form, with no distinct main axis, but they are invariably less branched than European shrubs. Others, however, perhaps the majority, are remarkable for having a single main axis, straight and branched only at the top, if at all: they resemble trees in miniature. The best examples of this habit are *Angylocalyx oligophyllus* Bak. f. (23, 3069) and *Sphenocentrum Jollyanum* Pierre (3306). The prevailing type of leaf is similar to that in the undergrowth tree stratum, entire or at most slightly serrate, with a long fine acumen.

A few shrubs are cauliflorous, e.g. *Drypetes molunduana* Pax and K. Hoffm. (3139, 3320) and *Angylocalyx*. There are no small palms in the shrub layer.

The herb stratum is even more unevenly developed than the shrub stratum. Large patches of the forest floor may be almost completely bare (Pl. I, phot. 1), elsewhere, especially in openings, it may be entirely concealed by the growth of herbs and small tree seedlings. On S.P. 1 and 2 Mr Ross made some counts of the number of shoots of herbs, seedling woody plants and ferns under 1 ft. (30 cm.) high on quadrats 3 m. sq. scattered at random. The number of shoots per quadrat varied from 40 to 492: the mean of S.P. 1 was 264, and on S.P. 2 190. Seedling woody plants greatly predominated, especially on those quadrats which had a large number of shoots. The density of the herb stratum seems to depend mainly on the shade cast by the canopy, but what part, if any, is played by root competition cannot be decided without experiment.

The height of the constituent species varies from the large Commelinaceae and ferns of 1 m. or more down to the creeping Geophilas, a few centimetres high only.

The ground herbs of the Mixed Forest may perhaps be regarded as belonging to two ecological elements or synusiae, (a) the specialized shade-loving species, and (b) the less specialized shade-tolerating species. Group (a) diminishes, or, at least, does not increase in abundance when the canopy is lightened and therefore attains its maximum abundance in undisturbed

primary forest. Group (b), which is comparable with the "wood marginal species" of the European Summer Forest (Salisbury, 1925), increases in abundance with increasing light intensity. It is thus better represented in both species and individuals in openings than in the darker parts of the primary forest. It reaches its maximum development in depleted forest and by paths and hauling roads. Some members of this group, e.g. some species of *Geophila*, need very little shade and may be found on waste ground on native farms in almost full sun.

The shade-loving species, e.g. *Trichomanes guineense* Schum. (3355) and several species of *Psychotria*, usually occur as solitary individuals and form an insignificant part of the herb layer as a whole. Most of the shade-tolerant species, on the other hand, are social and spread by runners or underground stolons: *Geophila* spp., *Palisota ambigua* (Beauv.) C. B. Clarke (3141) and other species sometimes form dense patches several square metres in extent, excluding all other vegetation.

The foliage of the ground herbs is much more varied than that of any other stratum. Features often common among the herbs of Tropical Rain Forests such as drip-tips, velvet surfaces and metallic colouring are absent, but variegation which is such a curiously widespread character in the leaves of the rain-forest ground flora is found in, for example, *Dracaena phrynioides* Hook. (228) and *Psychotria* sp. (3307). The only grass which is a normal constituent of the herb stratum, *Leptaspis cochleata* Thw. (3182, 3208), has leaves of the broadly elliptical shape characteristic of rain-forest grasses. A surprising feature of the herb stratum is the complete absence of species of *Selaginella*, which are usually very constant constituents of rain-forest undergrowth.

There is no moss stratum below the herb stratum, but ground mosses, e.g. *Fissidens* spp., are occasionally found on termites' nests or other places where the soil has been disturbed. With this exception, bryophytes are found only on the bark or leaves of living trees or shrubs or on fallen trunks.

(iii) *Climbers and hemi-epiphytes.*

The climbers of the Mixed Forest form two rather sharply contrasted synusiae, (a) the tall woody lianes reaching a height of 50 ft. (15 m.) or more above the ground, and (b), the small climbers growing to a height of not more than 25-30 ft. (8-9 m.).

Climbers of group (a) are exposed to strong illumination when full grown. As already mentioned, they spread from tree to tree in the canopy and bind it into a coherent mass. They also climb second-story trees, but seldom reach a height of more than about 70 ft. (22 m.) above the ground. They are not often found in the crowns of first-story trees, though *Agelaea trifolia* (Lam.) Gilg (38) was once noted in the crown of a tree at 110 ft. (34 m.).

Large climbers are always present in primary Mixed Forest, but do not become very abundant unless the canopy is disturbed. In natural or artificial

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openings and depleted forest they usually become extremely abundant, no doubt because they are light demanders.

Nearly all these climbers of group (a) are loose twiners. Many have specialized organs of attachment in their upper leafy part, e.g. adventitious roots in *Urera cameroonensis* Wedd. (3435), hooked branchlets in *Ancistrocladus guineensis* Oliv. (3151) and *Strychnos Afzelii* Gilg (3429, 3094), tendrils in *Paullinia pinnata* L. (3111). Other common lianes, e.g. *Agelaea trifolia* (Lam.) Gilg (38, 3127), *Combretum platypterum* (Welw.) Hutch. & Dalz. (3481), *Cyclocotyla oligosperma* Wernh. (3335, 3357), *Neuropeltis acuminata* (Beauv.) Benth. (3096), *Oncinotis gracilis* Stapf and *Uvaria anonoides* Bak. f. (3093, etc.), are less specialized morphologically. *Piper guineense* Thorn. (3041) is the only common member of this synusia which is a true root climber and does not twine at all.

Agelaea trifolia (Lam.) Gilg (38, 3127) is remarkable in that, though it is normally a tall woody climber, under open conditions it may grow into a small erect shrub flowering when about 1 m. high or less. Its ally, *Jaundea pinnata* Schellenb., is said to show a similar plasticity of habit (Hutchinson & Dalziel, 1931, vol. 1, p. 516).

In mature woody climbers of group (a) only the upper part of the plant, in and above the canopy, is leafy. The flowers are usually also borne only near the top, but a few species, e.g. *Pararistolochia flos-avis* (A. Chev.) Hutch. & Dalz. (3125, etc.), *Stephania Dinklagei* Diels (3372) and *Solanum inconstans* C. H. Wright (3373), are cauliflorous, bearing their flowers near the ground on the leafless part of the stem. The last-mentioned example is particularly curious in habit: the lowest portion of the stem forms a rooting rhizome running along the surface of the soil for some distance. The flowers are borne on short shoots arising from the rhizome and from the bare lower portion of the aerial stem. Climbing palms do not occur in the Mixed Forest.

Group (b) consists of small climbers which live in deep shade in the undergrowth and do not reach the canopy formed by the third-story trees. They are few in species and are mostly root-climbers. A few are twiners or climb by rooting and by twining. The commonest species are the fern *Lomariopsis guineensis* (Underw.) Alston (3178) and the aroids *Cercestis Dinklagei* Engl. (3369) and *Culcasia scandens* Beauv. (3368, 3464). The last two species do not always root in the ground and also occur as epiphytes. *Rutidea rufipilis* Hiern (3436) is one of the few dicotyledons which belong to this synusia.¹

A third synusia may be included with the climbers, viz. the hemi-epiphytes, represented only by the "strangling" figs, *Ficus* spp. (Pl. I, phot. 2). These plants are abundant in the Mixed Forest and represented by several species. They start life as epiphytes and send down roots to the ground. Afterwards they envelop the "host" tree with a lattice work of anastomosing roots and

¹ In some places this species appears to become a tall climber of group (a): at Amani (Tanganyika) it grows to 20 m. or more according to Brunnthaler (1914, Taf. 44).

usually kill it eventually and become large independent trees of the second, or perhaps sometimes the first, story.

(iv) *Epiphytes*.

The epiphytic vegetation of our area is relatively poor in individuals and strikingly poor in species. No comprehensive data as to the frequency of epiphytes in individuals can be given, but a general idea of the average number of species per tree and their abundance can be obtained from the observations on the two clear-felling plots given in Table III. The proportion of trees with vascular epiphytes (flowering plants and ferns) was 15 % on C.F.P. I and 24 % on C.F.P. II. The maximum number of species on any one tree was about thirteen. In the whole of the southern Shasha Reserve only twenty-one species of epiphytes were collected, and some of these were not seen actually in primary forest though they probably occurred there, but as some of the orchids were not in flower at the time of our visit and were not collected, the actual total is higher than this. It was estimated, however, that it was probably not more than thirty-five. Few observations were made on the epiphytes at Nikrowa: they seemed to be more abundant, but no species were collected there which were not also found in the Shasha Reserve.

The small number of species in these forests contrasts remarkably with the conditions in British Guiana. In the Moraballi Creek area, which is much smaller than the southern part of the Shasha Reserve, about 114 species of vascular epiphytes were collected, and the total number existing in the area was estimated at over 200 (Davis & Richards, 1933, p. 378). The average number of individuals per tree was probably greater than in the Shasha forest, but it may be noted that on a clear-felling plot the proportion of trees bearing vascular epiphytes was only 16 % and the greatest number of species per tree about eleven.

In the Mixed Rain Forest at Mount Dulit in Sarawak epiphytes were probably also rather more abundant, and there were certainly many more species than in the southern Shasha Reserve, though no data were obtained as to the number of species of epiphytes in the Dulit district as a whole. The proportion of trees on the clear-felling plots having epiphytes was, however, rather low, viz. 13 and 11 % respectively (Richards, 1936, p. 16), probably because they were on a steep-sided and rather exposed ridge, a situation unfavourable to epiphytes.

The comparatively poor development of the epiphytic vegetation in the Shasha forest is no doubt partly due to the severity of the dry season, but a small number of species of epiphytes seems to be characteristic of the African Rain Forest generally. For instance, Engler (1910, pp. 757-8) gives a list of the epiphytes in the primary lowland Rain Forest near Victoria in the Cameroons. The list, though no doubt not intended to be complete, is probably comparable with the data from the Shasha Reserve: it includes only twenty-six species, of which five are also found in our area.

Table III. *Epiphytes on trees on the clear-felling plots*
(Mixed Rain Forest Association)

All trees bearing epiphytic ferns or flowering plants are included in the following lists. The numbers in the first column are the reference numbers of the trees on Figs. 4 (C.F.P. I) and 5 (C.F.P. II).

No.	Species of tree	Total height m.	Height to first branch m.	Height to base of crown m.	Epiphytes
CLEAR-FELLING PLOT I					
1	<i>Diospyros insculpta</i> Hutch. & Dalz. (90, 155, etc.)	15.3	6.4	10.1	<i>Trichomanes Mettenii</i> C. Chr. (3437, etc.), 3.9–6.4 m.; 1 plot of <i>Asplenium africanum</i> Desv. (75, 3185) at 5.8 m.
2	Do.	20.7	1.4 9.8 (forked at base)	6.4 11.3	Two young plots of <i>Asplenium africanum</i> Desv. (75, 3185), at c. 10 m.; several plots of small orchid in crown
3	<i>Picralima umbellata</i> (Stapf) Stapf (8, 142, etc.)	21.7	5.8	8.8	<i>Polypodium lycopodioides</i> L. (267, 3008, etc.) on branch
4	<i>Diospyros confertiflora</i> Gürke (191, 3161, 3443)	25.0	17.1	17.1	Orchid at 10 m. Seedling orchid at c. 12 m.; <i>Calypstrochilum emarginatum</i> (Sw.) Schlecht. (246) at c. 24.5 m.
5	<i>Strombosia pustulata</i> Oliv. (3428, 3444) (or other sp. of <i>Strombosia</i>)	25.6	16.5	16.8	<i>Polypodium lycopodioides</i> L. (267, 3008, etc.) on trunk at 14 m. and abundant on upper part of trunk
6	<i>Diospyros confertiflora</i> Gürke (191, 3161, 3443)	27.1	13.7	18.6	Young <i>Asplenium africanum</i> Desv. (75, 3185) at 11.3 m. and in crown; orchid at c. 15.3 m.
7	<i>Xylopia Quintasii</i> Engl. & Diels (3434, etc.)	29.0	17.1	17.1	At 23–24 m.: <i>Angraecum subulatum</i> Lindl. (3022); <i>Calypstrochilum emarginatum</i> (Sw.) Schlecht. (246); young <i>Platyserium stemaria</i> (Beauv.) Desv. (120, 3423, 3451).
8	<i>Diospyros confertiflora</i> Gürke (191, 3161, 3443)	36.6	28.7	28.7	On branches: <i>Angraecum distichum</i> Lindl. (3462); <i>A. subulatum</i> Lindl. (3022); <i>Calypstrochilum emarginatum</i> (Sw.) Schlecht. (246) and another orchid
9	<i>Strombosia pustulata</i> Oliv. (3428, 3444) (or other sp. of <i>Strombosia</i>)	39.3	26.8	27.8	On upper branches: 2 spp. of orchids; <i>Loranthus</i> sp. ? <i>leptolobus</i> Benth. (= 3112?); <i>Platyserium stemaria</i> (Beauv.) Desv. (120, 3423, 3451)
10	<i>Lophira procera</i> A. Chev.	45.4	27.8	36.0	On trunk: young <i>Asplenium africanum</i> Desv. at c. 4 m. (75, 3185); <i>Angraecum subulatum</i> Lindl. (3022) at c. 20 m. On large branches: <i>Angraecum subulatum</i> Lindl. (3022); <i>A. distichum</i> Lindl. (3462); <i>Bulbophyllum oreonastes</i> Reichb. f. (3457); <i>Platyserium stemaria</i> (Beauv.) Desv. (120, 3423, 3451); <i>Polypodium Phymatodes</i> L. (3173, 3450) On small branches: <i>Bulbophyllum oreonastes</i> Reichb. f. (3457) and 3–4 other spp. of orchids

Table III (cont.). *Epiphytes on trees on the clear-felling plots*
(Mixed Rain Forest Association)

No.	Species of tree	Total height m.	Height to first branch m.	Height to base of crown m.	Epiphytes
CLEAR-FELLING PLOT II					
1	<i>Diospyros inculpta</i> Hutch. & Dalz. (90, 155, etc.)	7.0	3.1	3.1	<i>Polypodium lycopodioides</i> L. (267, 3008, etc.) and two large plots of <i>P. irioides</i> L. (86, 3404) in crown
2	Do.	7.9	2.4	2.7	<i>Angraecum pyriforme</i> Summerh. on branch (3476*)
3	<i>Conopharyngia penduliflora</i> Stapf (9, 3076, 3332)	8.2	3.9	4.9	Young fern and <i>Peperomia Mannii</i> Hook. f. (3477*) on lower branch
4	<i>Diospyros inculpta</i> Hutch. & Dalz. (90, 155, etc.)	11.0	5.2	6.7	<i>Asplenium africanum</i> Desv. (75, 3185) at 5.8 m. and a young plt. higher up
5	Do.	12.5	6.1	6.1	Several individuals of 1 sp. of orchid on lower branches
6	Do.	12.8	6.7	8.2	Small orchid on trunk at c. 5 m. On branches: young <i>Asplenium africanum</i> Desv. (75, 3185) at 7.0 m.; young <i>Calypstrochilum emarginatum</i> (Sw.) Schlecht. (246) and other spp. of orchids higher up
7	Do. (regenerating from stump c. 4 m. high)	14.0	7.9	10.1	Young <i>Ficus</i> sp. at top of stump On trunk at 6.4 m.: <i>Asplenium africanum</i> Desv. (75, 3185); <i>Polypodium irioides</i> L. (86, 3404) On lower branches: <i>Peperomia Mannii</i> Hook. f. (3477); <i>Polypodium irioides</i> L. (86, 3404); <i>P. lycopodioides</i> L. (267, 3008, etc.) 2-3 spp. of orchids on upper branches
8	Do.	15.2	5.2	7.0	Young plts. of <i>Asplenium africanum</i> Desv. (75, 3185) on trunk about 1 m. below first branch; young plts. of same fern in crown and two large plts. of <i>Polypodium irioides</i> L. (86, 3404) near base of first branch
9	Do.	15.9	9.2	11.0	Young <i>Asplenium africanum</i> Desv. (75, 3185) on branch
10	Do.	17.1	9.2	10.4	<i>Asplenium africanum</i> Desv. (75, 3185) at 4.6 m.; two spp. of orchids (one probably = <i>Angraecum pyriforme</i> Summerh. (3476)) on branches
11	Do.	17.7	8.5	11.9	Young <i>Asplenium africanum</i> Desv. (75, 3185) and <i>Polypodium irioides</i> L. (86, 3404) on trunk just below first branch
12	Do.	18.9	4.3	10.7	<i>Asplenium africanum</i> Desv. (75, 3185) at 8.8 and 10.4 m.
13	<i>Picralima umbellata</i> (Stapf) Stapf (8, 142, etc.)	19.2	3.7	10.1	<i>Asplenium africanum</i> Desv. (75, 3185) on branch
14	<i>Berlinia auriculata</i> Bth. (3158*, 3408, 3487*)	25.3	12.5	13.7	<i>Asplenium africanum</i> Desv. (75, 3185) at 12.5 m.; <i>Polypodium irioides</i> L. (86, 3404) on liane attached to tree at c. 14 m.

Table III (cont.) *Epiphytes on trees on the clear-felling plots*
(Mixed Rain Forest Association)

No.	Species of tree	Total height m.	Height to first branch m.	Height to base of crown m.	Epiphytes
CLEAR-FELLING PLOT II (cont.)					
15	<i>Berlinia auriculata</i> Benth. (3158*, 3408, 3487*)	25.3	12.5	14.3	Small orchids and young <i>Polypodium irioides</i> L. (86, 3404) on branches
16	Do.	25.9	12.5	18.6	On large branches: young <i>Asplenium africanum</i> Desv. (75, 3185); <i>Polypodium lycopodioides</i> L. (267, 3008, etc.); <i>P. irioides</i> L. (86, 3404), <i>Angraecum subulatum</i> Lindl. (3022) and another orchid, on small branches
17	Do.	29.9	14.3	18.6	On trunk: 6-7 spp. of orchids, including <i>Angraecum distichum</i> Lindl. (3462) at 6-7 m. and just below first branch On branches: <i>Angraecum subulatum</i> Lindl. (3022); <i>Calypstrochilum emarginatum</i> (Sw.) Schlecht. (246); <i>Polystachya odorata</i> Lindl. (3409), and about 6 other spp. of orchids, aroid (usually a climber); young <i>Asplenium africanum</i> Desv. (75, 3185); <i>Polypodium Lycopodioides</i> L. (267, 3008, etc.); <i>P. irioides</i> L. (86, 3404)
18	Do.	32.3	13.1	20.1	Orchid at 5.8 m. On branches at 17-20 m.: young <i>Angraecum subulatum</i> Lindl. (3022) and 3 other spp. of orchids; young fern On upper branches: <i>Polystachya odorata</i> Lindl. (3409); <i>Angraecum subulatum</i> Lindl. (3022) and about 4 other spp. of orchids; <i>Platynerium stemaria</i> (Beauv.) Desv. (120, 3423, 3451)

The ecological factors which seem to have the most marked effect on the distribution and composition of epiphytic vegetation are the age and nature of the bark of the tree, the humidity of the air and the illumination. Data on the vertical gradients of temperature and humidity in the primary forest will be given in Dr G. C. Evans's forthcoming paper.

The data from the clear-felling plots (Table III) show that epiphytes occur chiefly on the largest individuals of each species of tree, which indicates that effective colonization by epiphytes only begins late in the life of the tree.

It will be seen from Table III that though epiphytes are found on trees of all three stories, they become much more frequent above about 15 m., i.e. above the dense third story. This is no doubt entirely due to the higher light intensity in the upper levels. The great importance of the light factor is also shown very strikingly by the fact that some epiphytes which in the primary forest occur only in the crowns of very tall trees, e.g. *Loranthus leptolobus* Benth. (3112) and *Platynerium stemaria* (Beauv.) Desv. (120, 3433,

3451), may be found on isolated trees in clearings at only 1–2 m. above the ground, e.g. on Cola trees near villages in the Shasha Reserve. The greater abundance of epiphytes on C.F.P. II than on C.F.P. I is probably due to the more open first and second stories of the former (cf. Figs. 4 and 5). In openings in the primary forest epiphytes may continue to flourish for some time on fallen branches.

The effects of differences in the humidity (or rather saturation deficit) of the air in different habitats on the tree are difficult to disentangle from those of the light factor. Each species of epiphyte no doubt has its own particular limits of shade tolerance and drought resistance, but for practical purposes they may be considered as forming a number of groups with different requirements.

The epiphytes of the Moraballi Creek forests (Davis & Richards, 1933, pp. 380–1) were grouped into four “societies” or *synusiae* (a) shade epiphytes, (b) sun epiphytes, (c) extreme xerophilous epiphytes, (d) epiphytic parasites (Loranthaceae). All four groups are represented in the Shasha Mixed Forest, but the number of individuals and species concerned is so small that it is doubtful whether the term society should be applied to them.

(a) *Shade epiphytes*. These are found on third-story trees below the canopy and to a less extent on the lower part of the trunks of larger trees. They live under conditions of deep shade and low and relatively constant saturation deficit. They are sometimes almost absent and the number of individuals is always small. Some of the species may appear again in the crowns of trees with very dense foliage. The species belonging to this group are the filmy ferns, *Trichomanes erosum* Willd. (111, 3438), *T. Mettenii* C. Chr. (183, 3415, 3437) and *Asplenium africanum* Desv. (75, 3185), a nest epiphyte with coriaceous leaves resembling the well-known *A. nidus* L. This species also belongs to the next group: here it seldom reaches its full size. Rarer species are *Angraecum pyriforme* Summerh. (3476), *Asplenium hemitomum* Hieron. (230) (seen only by the river), *Peperomia Mannii* Hook. f. (3317, 3477) (creeping, leaves succulent) and *Polypodium irioides* L. (86, 3404) (this is more often a member of the next group).

(b) *Sun epiphytes*. These occur on the larger branches and sometimes the trunks of first- and second-story trees or exceptionally tall individuals of third-story trees. They live under conditions of relatively strong illumination and variable saturation deficit. They need a high degree of drought resistance and most of them are markedly xeromorphic. The commoner species are the ferns, *Asplenium africanum* Desv. (75, 3185), *Polypodium irioides* L. (86, 3404) (nest epiphyte, leaves very coriaceous), *P. lycopodioides* L. (267, 3008, etc.) (creeping, rhizome very scaly), *P. Phymatodes* L. (3173, 3450) (rhizome creeping, leaves coriaceous), and *Platyserium stemaria* (Beauv.) Desv. (120, 3423, 3451) (bracket epiphyte, leaves coriaceous); also the orchids *Angraecum distichum* Lindl. (3462), *A. subulatum* Lindl. (3022) and *Calypstrochilus emarginatum* (Sw.) Schlecht. (246). Rarer species are—ferns: *Davallia Vogelii* Hook. (266), *Oleandra*

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distenta Ktze. (268) and *Vittaria guineensis* Desv. (231) (seen only on a tree overhanging the Oni river, but may also occur in the interior of the forest); orchids: *Bulbophyllum oreonastes* Reichb. f. (3457), *Polystachya odorata* Lindl. (3409) and a number of unidentified species; other flowering plants: *Rhipsalis Cassythia* Gaertn. (138) and perhaps *Peperomia Mannii* Hook. f. (3317, 3477).

(c) *Extreme xerophilous epiphytes*. These, in primary forest, are found only on the upper and finer branches of the first story, and taller second-story trees where they are exposed to the conditions of temperature and humidity prevailing in the open practically unmodified. This group is difficult to separate from the last to which all its species also belong, and an exact list of it cannot be given. *Platycerium stemaria* (Beauv.) Desv. (120, 3423, 3451) is a characteristic member.

(d) *Epiphytic parasites*. This group is represented by *Loranthus leptolobus* Benth. (3112) and *L. constrictiflorus* Engl. (36). The former is probably common and occurs on a variety of hosts, the latter was found once only, on *Azelia bipindensis* Harms (25), in depleted forest, but probably also occurs in the primary forest.

The societies of epiphytic bryophytes and lichens were not closely studied from the ecological point of view, but there appeared to be societies of shade, sun and extreme xerophilous epiphytes corresponding to groups (a), (b) and (c) above: in addition, there was a society of epiphyllae found on the leaves of trees and shrubs in the undergrowth.

The shade society of bryophytes is found chiefly on shrubs and on the finer branches of undergrowth trees: the lower part of the larger trunks is usually bare or only sparingly colonized by bryophytes. This society becomes conspicuous in the damper parts of the forest, near swamps, etc., but is often only feebly represented. The moss *Pilotrichella communis* C.M. (3147, 3479), which hangs down from the branches in long streamers, is characteristic and often very abundant, but the majority of the species are Hepaticae (*Plagiochila* spp., Lejeuneaceae). Lichens are rare.

The sun society occurs on the trunks and larger branches of trees above the canopy. It consists of many species of Hepaticae (chiefly Lejeuneaceae) and lichens, with a few mosses (*Pilotrichella* sp. sparingly).

The extreme xerophilous society on the twigs and upper branches includes many lichens, a few Hepaticae (Lejeuneaceae, *Frullania nodulosa* (R., B. & N.) Nees (3062), *Plagiochila* sp. (3060)) and mosses, e.g. *Macromitrium* sp. (3061).

Epiphyllae are found chiefly on leaves in the lower part of the undergrowth, and are rare even on trees of the first story. For instance, on the two clear-felling plots only three trees had epiphyllous Hepaticae on their leaves.

The epiphyllous community is not well developed in the Mixed Rain Forest, and only becomes at all abundant in moist sheltered places. The number of species is small and most of them are Hepaticae (*Radula* spp., Lejeuneaceae).

It is doubtful if it is possible to speak of a definite succession occurring

among the epiphytes of the Mixed Forest, but certain species probably prepare the way for others, for instance, some vascular plants probably only establish themselves in tufts of Hepaticae. No definite observations were made on this point, however.

(v) *Heterotrophic plants.*

In the Tropical Rain Forests of America and Asia a society of saprophytic flowering plants is found, consisting of members of the Gentianaceae, Triuridaceae, Burmanniaceae, etc. (Davis & Richards, 1933, p. 372; Richards, 1936, p. 17). Saprophytes belonging to these families are frequent in some parts of the African Rain Forest, and species of *Voyria* (Gentianaceae), *Sciaphila* (Triuridaceae) and *Gymnosiphon* (Burmanniaceae) have been recorded from localities in Southern Nigeria (Hutchinson & Dalziel, 1931, 1936). In spite of careful search, however, none of these plants could be found in the forests of our area. The growth of these little saprophytes is very dependent on weather conditions, so it is probable that some of them might have been found at other seasons than the period of the expedition. Saprophytic fungi were abundant.

The only totally parasitic flowering plant in the Mixed Forest was *Thonningia sanguinea* Vahl (3011, 3421) (Balanophoraceae). It is a root parasite on the roots of a large variety of trees, though showing a distinct preference for *Lophira procera* A. Chev. The inflorescences project a few centimetres above the surface of the soil. This is a very constant, but not very abundant, member of the Mixed Forest Association.

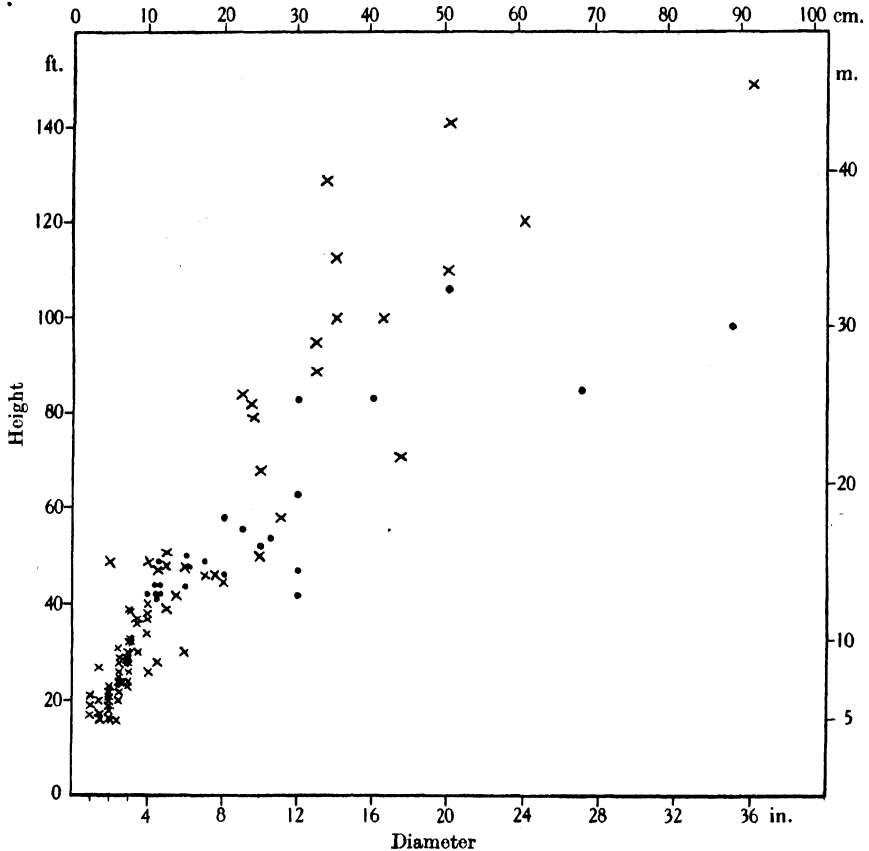
(c) *Floristic composition*

The floristic composition of the Mixed Forest was studied by means of three sample plots, two situated near the Cambridge Expedition camp in the Shasha Reserve and one in the Okomu Reserve near Nikrowa. Each plot was 160,000 sq. ft. (1.49 ha.) in area. The sides were marked out by paths cut through the undergrowth using a prismatic compass and a measured rope: cross paths were also cut dividing each plot into strips 100 ft. (30.5 m.) wide. On each plot the girth and vernacular name of all trees 12 in. (30 cm.) girth and over was recorded with the help of a trained native forest guard. The shrubs and herbs were then listed with the usual frequency symbols (a., f., etc.), but the lists cannot be claimed to be very accurate owing to the difficulty in distinguishing between shrubs and herbs not in flower and young trees and lianes. No practical method was available for listing the climbers. The epiphytes on the clear-felling plots (parts of S.P. 2 and 1 respectively) have already been considered. On each sample plot a pit was dug to examine the soil profile and a monolith was collected: descriptions of these profiles and analyses of the soil samples have already been given (pp. 15-18).

The vernacular names of the trees (mostly Yoruba, a few Bini) used by the

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forest guard were found to be on the whole constant and reliable. Our task in working out the botanical equivalents of the names was much simplified by the previous work by officers of the Nigerian Forestry Department, but we tried to collect specimens of as many as possible of the species found on the plots. By repeated visits we succeeded in obtaining flowering material of a considerable proportion actually from the plots, and material of the majority of



A large proportion of the names used by our enumerator seemed, *within the limited areas in which we were working*, to correspond to a single species only. Others corresponded to a genus or group of similar species sometimes in more than one genus, e.g. Sapo sapo = *Anthocleista* spp., Idagbon = *Pausinystalia* spp. and the closely allied *Corynanthe pachyceras* K. Schum. (the prefixes "Abo" and "Ako" do not always seem to represent constant groups of species within these genera). It must be remembered that, while over an extensive district the same name may be applied to a number of similar species, within a limited area it may happen that only one or two of these are present. Thus Erun = *Erythrophleum* spp.; in our area, however, *E. micranthum* Harms was apparently the only species of the genus present, but in a savannah area the botanical equivalent would be *E. guineense* Don. Similarly, Oganwo = *Khaya* spp., but on our plots it is probably equivalent only to *K. ivorensis* A. Chev. The equivalents given in this paper are only intended to apply to our sample plots and should be used only with caution in other areas.

The sites, etc., of the three Mixed Forest plots were as follows:

S.P. 1. Shasha Reserve, about 8 km. north of Akilla. A square plot 400 (122 m.) \times 400 ft., situated on nearly level ground, which within a few hundred metres of the edge of the plot slopes down by a steep bank to a stream (the Erioloma). Partly good forest with clean undergrowth, but on the remainder there were several openings. These seemed to be natural, as there were no cut stumps or other signs of timber felling. The primary nature of this plot is, however, less certain than that of *S.P.s* 2 and 3 (cf. p. 20).

S.P. 2. Near Eluju village, Shasha Reserve, about 5 km. north-west of Akilla and about 6 km. south-west of *S.P.* 1. A square plot, 400 (122 m.) \times 400 ft. on a low tongue of nearly level dry land between two large areas of swamp. The permanent water-table is probably only about 2-3 m. below the soil surface, a fact which is reflected in the presence of some swamp-loving species in the undergrowth, e.g. young *Raphia* palms, but the plot is never flooded. Timber was being worked in the neighbourhood, but the plot itself had apparently never been interfered with in any way, its immunity probably being due to its awkward situation for extracting timber.

S.P. 3. Okomu Reserve, about 6 km. north of Nikrowa Camp (about 100 km. west of *S.P.* 1 and 4). Situated on ground sloping gently down to a small pond. Originally a plot 400 (122 m.) \times 400 ft. was marked out, but the lowest strip was found to include so much of the marshy ground surrounding the pond that it was rejected and another strip 400 \times 100 ft. nearby was marked out in its place. The figures for this strip and the remainder of the original square plot have been added together and treated as a single plot. This plot was all fine forest with clear undergrowth (Pl. I, phot. 1): it formed part of a patch of primary forest about 2.5 times its own area.

The results of the enumerations are given in full in Tables VI-VIII and a summary of the main data is given in Tables IV and V. The data for the sample

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plot in Fresh-water Swamp Forest (S.P. 4) (p. 42) have also been included in the latter tables. For comparison with the data for Guiana and Sarawak the original measurements, in the form of girths, have been converted to diameters and grouped into 4 in. classes. Measurements of girth were made at breast height or above the buttresses.

The significance of the data for the three Mixed Forest plots will be best seen by comparing them with the other comparable data for the African Rain Forest, those of Jentsch (1911) for various localities in the Cameroons and those of Mildbraed for the Likomba Forest, near the foot of Cameroons Mountain (1930 *a*, 1930 *b*) and for Fernando Po (1933), also with the data for Mixed Forest plots in British Guiana (Davis & Richards, 1934, pp. 117-18, Tables I and IV, etc.) and Sarawak (Richards, 1936, p. 21 and Appendix).

Jentsch's plots were situated in various types of forest, primary and secondary: his plots II, V and VII are the most suitable for the present comparison, as they represent typical lowland rain forest and are stated to show no signs of felling or other human interference. These plots are 0.5 ha. in area. The height as well as the diameter of all trees over 7 cm. diam. was measured but only the vernacular names of the species are given. Mildbraed's fifteen plots at Likomba were all 1 ha. in area. The diameter of all trees 30 cm. (=approximately 12 in.) diam. and over was measured. Only the botanical names of the species are given in the published results, and it is not clear whether the original enumeration was carried out by means of vernacular names or not. His Fernando Po plot was also 1 ha. All trees down to 10 cm. (=4 in.) were felled and measured and the smaller undergrowth was listed. Botanical names only are given and apparently herbarium specimens of each species were collected.

The British Guiana plots are comparable in all respects with the Nigerian plots: the Sarawak plots are also comparable except that only trees 8 in. (20 m.) and over were enumerated.

The number of trees 4 in. (10 cm.) and over per hectare on the three Nigerian plots varies considerably, but the mean (474) is close to the number on the British Guiana Mixed plot (432). The differences between the three Nigerian plots are due chiefly to the variation in numbers in the smaller size classes, the numbers of larger trees varying less widely. The number of trees 16 in. (41 cm.) and over is, however, rather lower on S.P. 1 than S.P. 2 and 3. Compared to any of the Guiana plots, except the Mora (swamp) plot, the number of trees in this size class is low on all the Nigerian plots: this agrees with the conclusion from the clear-felling plots (p. 23) that trees of the two upper stories are less densely distributed in the Nigerian forest. This does not seem to be a general characteristic of the African Rain Forest, as on Jentsch's three plots the numbers of trees over 40 cm. diam. (approximately equivalent to 16 in.) are 90, 84 and 92 per hectare respectively, as compared with 60 on the Guiana Mixed plot and 42, 48 and 47 on S.P. 1, 2 and 3 respectively. On

Mildbraed's Fernando Po plot the number (40 cm. and over) was 76, but on many of his Likomba plots the number was even lower than on our Nigerian plots. Most of the Likomba plots were almost certainly depleted to some extent: Mildbraed, in fact, states that on one of his plots there was a cut stump.

The small number of trees of 16 in. and over on the Nigerian plots may have been caused by depletion in the past, but it may, on the other hand, be due to some natural factor, such as the relatively unfavourable climate (p. 9) or the effect of tornadoes (p. 7). The fact that on the Sarawak Mixed plot, on which it is almost certain that there had never been any felling, the number of trees of 16 in. and over was as low as 43 per hectare shows that a small number of large trees need not necessarily indicate depletion.

The figures for the number of tree species per plot show that the Nikrowa plot (S.P. 3) is much richer in species than either of the plots in the Shasha Reserve (S.P. 1 and 2). The greater richness of S.P. 3 compared with S.P. 2 is also clearly shown in Fig. 7, where curves are given of the relation of the number of species to area *within* these two plots (and S.P. 4 the Fresh-water Swamp plot). Each of these plots was enumerated in four separate strips (each 400×100 ft. = 122×30.5 m.). Each strip is treated as a separate unit, then by taking the average number of species on the four strips, on the six possible combinations of two strips, on the four possible combinations of three strips, and the number on the whole plot, four points are obtained through which a species/area curve can be drawn. It will be seen in Fig. 7 that at the area of the whole plot the curve for S.P. 2 (and S.P. 4) is flattening out perceptibly, while that for S.P. 3 is still rising steeply. For the latter, therefore, the area sampled is less than the "minimal area" for trees 4 in. diam. and over.

The species/area curves for trees 12 in. (30 cm.) diam. and over make it possible to compare the richness in species on these Nigerian plots and on Jentsch's and Mildbraed's: this cannot be done directly owing to the difference of area in the three sets of plots. Reading from these curves, the numbers of species 12 in. and over on 0.5 ha. are 16 and 21 on S.P. 2 and 3 respectively: these figures can be compared with 34 species of this size-class on Jentsch's plot V (0.5 ha.).¹ The numbers of species on 1 ha., according to the curves, are 22 and 32 on S.P. 2 and 3 respectively. On Mildbraed's Likomba plots (each 1 ha.) the greatest number of species is 24 and the least 12: the mean for the 15 plots is 17. The Fernando Po plot (also 1 ha.) has only 15 species, and is therefore poorer than our S.P. 2 or 3: probably it is also poorer than S.P. 1, but an exact comparison cannot be made, as the data for constructing a species/area curve were not obtained for that plot.

On the available data then, the Mixed Forest of an area seems to be less rich in species than the richer forests of the Cameroons but richer than the

¹ For Jentsch's other plots only the numbers of species of trees of 7 cm. diam. and over are given.

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poorer forests. Compared with both the British Guiana and the Sarawak Mixed Forest plots, all three Nigerian plots are very poor in species: the relative poverty is particularly marked among the small (third-story) trees.

There is no obvious reason for the much greater richness of the Nikrowa plot compared with the two Shasha plots, which are in a similar climate and

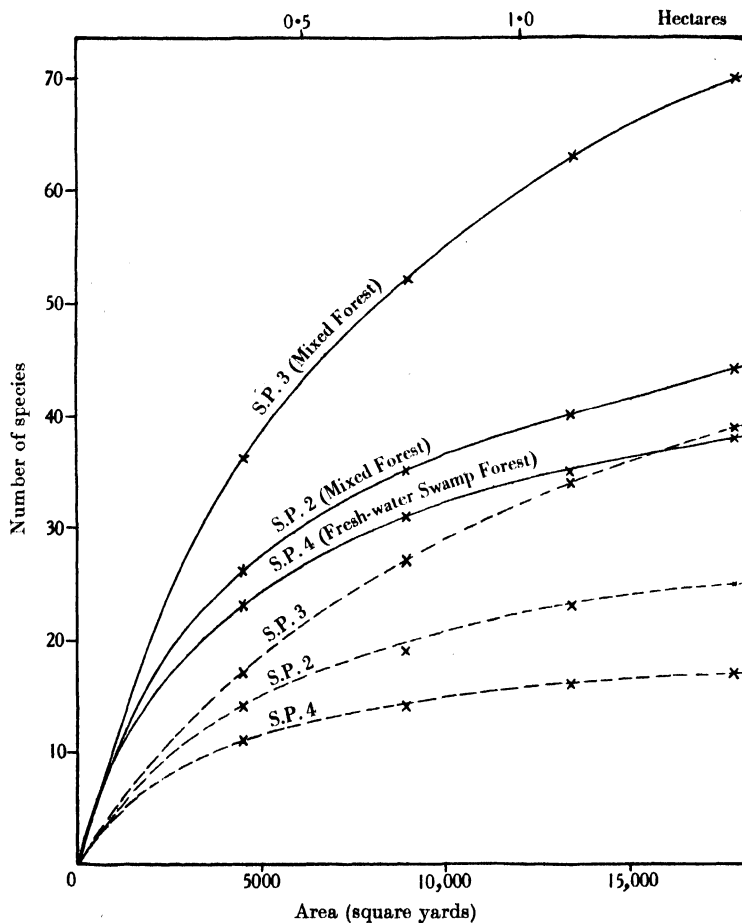


FIG. 7. Species/area curves for Sample Plots 2, 3 and 4.

Continuous lines = trees 4 in. (10 cm.) diameter and over.

Broken lines = trees 12 in. (30 cm.) diameter and over.

situated only a little over 100 km. apart. Possibly it may be connected with the difference of soil. The Nikrowa plot was on a porous brown sand and it may be significant that on the richest in species of the five Guiana plots (Greenheart) the soil was also a brown sand.

In the forest types in British Guiana and Sarawak a low number of species

was correlated with the more or less marked dominance of a single species. On the three Nigerian plots, in spite of the relatively small number of species, little tendency to single-species dominance is shown, generally speaking. The tendency is much more marked among the smaller trees—the size classes under 16 in. (41 cm.) diameter—than among the larger, but while the degree of single-species dominance in the 16 in. (41 cm.) and over class shows some correlation¹ with the richness in species (number of species 4 in. and over), the degree of dominance in the under 16 in. class shows none. On two of the plots the degree of dominance in the 16 in. and over class is greater than on the Guiana Mixed plot and on one it is less. In the under 16 in. class, on the other hand, the degree of dominance on all the plots was greater than on the Guiana Mixed plot. Even on the Mora and Wallaba plots in Guiana, which show a very high degree of dominance among the trees of 16 in. and over, the degree of dominance among the smaller trees is less marked than on these Nigerian plots. On each of the three plots the most abundant species in the 16 in. and over class is different from that in under 16 in. class. According to information given to the writer by Mr J. R. Ainslie the only districts of the Nigerian Rain Forest where there is marked dominance of a single first-story species are in Calabar and Ogoja Provinces: in these *Mimusops Djave* Engl. occurs “somewhat gregariously and forms forests quite resembling good Dipterocarp forest of the East”.

In the actual floristic make-up of the tree strata, the three plots show considerable differences. Though many species are common to all three, the proportions in which they occur vary widely. Thus only three species are represented by ten or more individuals 4 in. diameter or over on all three plots (Table V). The evidence suggested that the differences were not due to “sampling errors”, but that the three plots represented more or less widely distributed types or facies. As far as our reconnaissance went, it appeared that forest like S.P. 1 was widespread in the southern Shasha Reserve and forest like S.P. 3 widespread in the Okomu Reserve.

In the Likomba forest Mildbraed found a striking preponderance of certain species in certain areas, but considered that the forest formed a non-homogeneous mixture rather than a number of separate associations. His reasons for this conclusion were that the preponderance of particular species did not seem to be correlated with particular edaphic factors (though he publishes no data on these), and the abundance of particular species of trees did not seem to be correlated with differences in the composition of the undergrowth.

On our plots it is evident that there are considerable differences in edaphic conditions (pp. 15–18), though the evidence is not sufficient to decide whether the floristic composition is really correlated with these differences or not.

With regard to the shrub and herb layers, however, an examination of the lists at the end of Tables VI–IX will show that these differ at least as much as the tree layers.

¹ The Swamp Forest plot (S.P. 2) may be included in the series for this comparison.

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It must be concluded therefore that the data from these sample plots suggest that the Mixed Forest Association consists of a number of facies, differing chiefly in the proportions in which the species occur. The "Agba-Okan forest" described by Sykes (1930) from the Benin Sands region (to the east of the Okomu Reserve) is probably another such facies: it is associated with sandy soils and two of the most characteristic species are *Gossweiler-*

Table IV. *Comparison of sample plots*

Sample plot	Nigeria				Mixed Forest British Guiana	Mixed Forest Sarawak
	Fresh-water Swamp Forest	Mixed Forest				
		4	1	2		
No. of trees 4 in. (10 cm.) and over on plot	536	606	781	582	644	—
Do. per hectare	360	407	523	390	432	—
No. of trees 8 in. (20 cm.) and over on plot	241	277	341	317	330	261
No. of trees 16 in. (41 cm.) and over on plot	72	63	71	70	90	62
Do. per hectare	48	42	48	47	60	44
No. of "species"* 4 in. (10 cm.) diam. and over on plot	38	34	42	70	91	—
No. of "species"* 8 in. (20 cm.) diam. and over on plot	23	25	29	51	57	98
No. of "species"* 16 in. (41 cm.) diam. and over on plot	11	13	16	31	31	32
Most abundant species 4 in. (10 cm.) and over	<i>Spondianthus</i> sp. cf. <i>ugandensis</i>	<i>Diospyros</i> <i>insculpta</i>	<i>Rinorea</i> sp. cf. <i>oblongifolia</i>	<i>Strombosia</i> <i>retivenia</i> †	<i>Pentaclethra</i> <i>macroloba</i>	—
Percentage	27	38	20	30‡ (or less)	11	—
Most abundant species 8 in. (20 cm.) and over	<i>Spondianthus</i> sp. cf. <i>ugandensis</i>	<i>Diospyros</i> <i>insculpta</i>	<i>Strombosia</i> <i>pustulata</i> §	<i>Strombosia</i> <i>retivenia</i> †	<i>Pentaclethra</i> <i>macroloba</i>	"Medang lit"
Percentage	24	27	23‡ (or less)	35‡ (or less)	13	5
Most abundant species 4– 15 in. (10–40 cm.)	<i>Spondianthus</i> sp. cf. <i>ugandensis</i>	<i>Diospyros</i> <i>insculpta</i>	<i>Rinorea</i> sp. cf. <i>oblongifolia</i>	<i>Strombosia</i> <i>retivenia</i> †	<i>Pentaclethra</i> <i>macroloba</i>	—
Percentage	29	42	22	34?	14	—
Most abundant species 16 in. (41 cm.) and over	<i>Mitragyna</i> <i>stipulosa</i>	<i>Berlinia</i> <i>auriculata</i>	<i>Casearia</i> <i>bridelioides</i>	<i>Pausiny- stalia</i> sp. or spp.†	<i>Eschweilera</i> <i>Sagotiana</i>	2 spp. each
Percentage	36	35	21	14 (or less)	16	10

* As some of the vernacular names may include more than one species (cf. Tables VI-IX) these figures are minimum numbers.

† Cf. Table VIII.

‡ Percentage calculated on the assumption that only one species of these genera are present on this plot.

§ Cf. Table VII.

|| See footnote, p. 45.

dendron balsamiferum Harms (Agba) and *Cylicodiscus gabunensis* Harms (Okan). How well defined these facies are and the nature of the edaphic factors with which they are correlated are questions which must be left for future investigation. In any case, however, the differences between them are of a smaller degree than those between the five forest "types" described from British Guiana or the two from Sarawak.

Table V. *Tree species represented by ten or more individuals of 4 in. (10 cm.) diam. and over on sample plots*

On equivalence of vernacular names, cf. Tables VI-IX.

+ = present in ten or more individuals.

p = present in smaller numbers.

	Sample plot	Mixed Forest			Fresh-water
		1	2	3	Swamp Forest
Abura	<i>Mitragyna stipulosa</i> *	—	—	—	+
Agbawu	<i>Musanga Smithii</i>	+	p	p	p
Ahun	<i>Alstonia congensis</i>	—	—	p	+
Apado	<i>Berlinia auriculata</i>	+	—	—	—
Apako	Annonaceae	—	p	+	—
Atole	<i>Sapium ellipticum</i>	p	p	+	p
Awasa Aragba	<i>Bridelia micrantha</i>	—	—	p	+
Ebo	<i>Casearia bridelioides</i>	p	+	p	+
Erin	<i>Picralima umbellata</i>	+	+	p	p
Erun	<i>Erythrophleum micranthum</i>	p	+	p	—
Esunsunapon	<i>Diospyros confertiflora</i>	+	+	+	p
Esunsunesunsun	<i>D. atropurpurea</i>	—	—	+	—
Idagbon, Abo	<i>Pausinystalia</i> or <i>Corynanthe</i> sp. (cf. Tables VI-IX)	+	p	+	— ?
Idapopo	<i>Conopharyngia penduliflora</i>	+	—	p	—
Itako	<i>Strombosia pustulata</i> (and other spp. ?)	p	+	+	—
Itako pupa	<i>Strombosia retivenia</i> (and <i>S. grandiflora</i> ?)	—	—	+	—
Jesebe	<i>Discoglypemma caloneura</i>	—	p	+	p
Kalado	<i>Homalium</i> sp. (? <i>africanum</i>)	—	—	—	+
Obonekute	<i>Spondianthus</i> sp. cf. <i>ugandensis</i>	—	—	—	+
Odogbo	<i>Anthostemma Aubryanum</i>	—	—	—	+
Odoko	<i>Scottellia kamerunensis</i> and/or <i>Scottellia</i> n.sp.	+	+	+	+
Ogwagwa	<i>Diospyros chrysantha</i>	+	+	p	—
Oloda	—	—	p	+	—
Olofun	<i>Guarea cedrata</i>	—	—	+	p
Ombe	<i>Rinorea</i> sp. cf. <i>oblongifolia</i>	+	+	—	p
Opalifon	<i>Xylopia Quintasii</i>	+	+	p	+
Opepe ira	<i>Sarcocephalus nervosus</i>	—	—	—	+
Osho pupa	<i>Enantia chlorantha</i>	—	+	p	—
Oshun	<i>Diospyros insculpta</i>	+	+	+	p
Shekameja	—	—	p	—	+
Telegon	<i>Casearia</i> n.sp.	p	+	—	p

* See footnote, p. 45.

(2) FRESH-WATER SWAMP FOREST (EDAPHIC CLIMAX)

The lagoons and waterways of south-western Nigeria offer excellent opportunities for studying the primary hydrosere, all stages between open water and closed swamp forest being represented in abundance. On the banks of some of the larger rivers the stages of this succession can be seen in a telescoped form as a zonation; thus on the lower part of the Osse (near Nikrowa) as many as four zones can be observed, viz.

- | | | | |
|--|-------------------------------------|--|----------------------------------|
| A. Submerged aquatic vegetation and free-floating "sudd" of <i>Pistia</i> , etc. | B. Community of <i>Pandanus</i> sp. | C. Community consisting chiefly of <i>Raphia</i> sp. (or spp.) (palms) | D. Tall Fresh-water Swamp Forest |
|--|-------------------------------------|--|----------------------------------|

Time did not allow a close study of the hydrosere, but its general course seemed to be as follows:

- | | | | |
|--|--|---|---|
| 1. Aquatic communities: Submerged vegetation (<i>Ceratophyllum demersum</i> L., <i>Utricularia</i> spp. etc.). Free-floating "sudd" (<i>Pistia Stratiotes</i> L., <i>Salvinia nymphellula</i> Desv. (3216), grasses, etc.). Floating leaf vegetation (<i>Nymphaea Lotus</i> L. etc.). | → 2. Herbaceous marsh → vegetation: various communities, including in some places communities of <i>Cyperus Papyrus</i> L. and of <i>Pandanus</i> sp. etc. | 3. Palm swamp, dominated by <i>Raphia</i> sp. (or spp.) | → 4. Closed Fresh-water Swamp Forest with few or no palms |
|--|--|---|---|

In a discussion of the primary hydrosere of the Gold Coast, Chipp (1927, pp. 61-4) describes a "Lagoon marsh associates", a "Calamus-Ancistrophyllum-Raphia (palm) associates" and a "Tarrietia-Anopyxis associates". The first two of these seem to be analogous to stages 2 and 3 respectively in the above scheme. The last corresponds with what is here termed Fresh-water Swamp Forest, though the two characteristic species are not prominent in our area: *Anopyxis ealaensis* Sprague is not common in Nigeria (Kennedy, 1936, p. 50), while *Tarrietia utilis* Sprague seems to be quite absent.

In the present paper only the last stage of the succession will be dealt with, a type of high forest which is flooded in the wet season and waterlogged to within a few centimetres of the soil surface during the rest of the year. Where it abuts on gently rising ground a gradual transition from it to Mixed Rain Forest may be seen, but it does not appear to show any appreciable tendency to develop into this or any other type of vegetation. In the opinion of the present writer it is doubtful if it ever would do so without a change in the water level due to some external cause and it is therefore here regarded as an edaphic climax.

The sample plot of this type of forest, S.P. 4, was situated in the broad swampy valley of a small stream (the Erioloma) about 8 km. north of Akilla and within a few hundred metres of S.P. 1 (Mixed Forest). The following account will refer chiefly to this plot and the forest in its immediate neighbourhood,

as it was impossible to explore the swamp forest as extensively as the dry land forest. Several types of Swamp Forest could no doubt be distinguished, depending on variations in soil, etc., but the forest in which the sample plot was situated seemed to represent a fairly constant type which was widespread in the stream valleys in the southern Shasha Reserve and other parts of south-western Nigeria.

As has already been mentioned, timber is seldom felled in the swamp forest in our area,¹ and there is little evidence of interference of any kind.

The soil on S.P. 4 was a soft, sticky, greyish clay. The following is a description and analysis of the soil profile:

A. 33². Primary Fresh-water Swamp Forest, S.P. 4, by the Erioloma stream about 8 km. north of Akilla, Shasha Forest Reserve.

Description:

Horizon I. 0-2 in. (0-5 cm.). Dark brown. Large amounts of humus, both as decaying plant matter and intimate. Light loam. Nutty. Loose and porous. Root mat developed. Much vegetable matter on surface. Sharply delimited below.

Horizon II. 2-9 in. (5-23 cm.). Lighter brown with red mottlings. Humus well defined. Clay. Nutty. Compact. Iron accumulation as mottlings. Few roots. Clearly delimited below.

Horizon III. 9-14 in. (23-36 cm.). Grey. Humus still evident. Heavy clay. No structure as the subsoil has been puddled. The water table came into the bottom of this horizon.

Type: Tropical Yellow Earth.

Analysis:

Horizon	II	III
Loss on ignition	17.6	12.4
Mechanical analysis (as percentage of mineral matter):		
Coarse sand	21.2	20.7
Fine sand	35.7	32.8
Silt	14.2	16.0
Clay	27.8	29.2
Clay analysis:		
SiO ₂ (%)	43.3	39.1
Al ₂ O ₃ (%)	27.4	40.0
Fe ₂ O ₃ (%)	9.45	6.06
SiO ₂		
Al ₂ O ₃	2.7	1.7
SiO ₂		
Al ₂ O ₃ + Fe ₂ O ₃	2.2	1.5
Organic analysis:		
Carbon (%)	3.8	0.22
Nitrogen (%)	0.04	0.002
C/N	13.8	15.2
pH	6.8	6.0

¹ In some districts timber of Abura, *Mitragyna stipulosa* Ktze. has been extracted. Rice cultivation and dry season farming are practised in Swamp Forest in Warri Province.

² Campbell's (1936) reference number.

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Humus is thus more abundant than in any of the Mixed Forest soils (pp. 15-18), though there is no tendency to peat formation such as is found in some types of tropical swamp forest. The water of streams rising in the swamp forest was coloured yellowish brown, but not as deeply as that of the "black water" streams of some tropical regions (Richards, 1936, p. 26).

(a) *Structure*

The Fresh-water Swamp Forest differs in structure from the Mixed Forest chiefly in its on the whole more open canopy, its dense tangled undergrowth and, above all, in its greater irregularity. Tall trees are abundant, but they are not evenly distributed. Areas of high forest casting a deep shade are mixed with tangled thickets of bushes and lianes in which tall trees are thinly scattered or absent. These thickets (Pl. II, phot. 5) are formed chiefly of *Leea guineensis* Don, a straggling shrub with prop roots which grows to a height of 6 m. or more: in parts of the plot it formed an almost pure growth excluding nearly all smaller undergrowth. Even where *Leea* is absent, the undergrowth was generally so thick and impenetrable as to make the enumeration of the trees difficult. In some places, however, the undergrowth is very scanty and there are large patches of almost bare soil or pools of muddy water. This extreme variability in the closeness of the canopy and density of the undergrowth (the second doubtless depending on the first) seems to be related, at least partly, to small inequalities of the ground level. On the plot the ground level was highest on the side adjoining the stream: here there was a closed canopy and relatively thin undergrowth. Further away from the stream the ground level was so low that there were many pools of standing water even at the end of the dry season: there the canopy was much more open and *Leea* thickets were numerous.

This extreme irregularity of structure (which no doubt repeats itself as a regular pattern if large enough areas are considered) is reminiscent of that of secondary forest. The frequent breaks in the canopy make possible the growth of such of the light-demanding secondary forest species as can tolerate the peculiar edaphic conditions. Thus, *Bridelia micrantha* Baill. (3282) is an abundant tree in quite undisturbed swamp forest as well as in secondary forest. On the other hand, the swamp forest also offers suitable habitats to shade-loving species, e.g. *Trichomanes erosum* Willd. (111, 3438) is a common epiphyte on the tree trunks.

The number of trees 4 in. (10 cm.) diameter and over is, as might be expected, lower than on any of the three Mixed Forest plots, but it is surprising to find that there are 72 trees 16 in. (41 cm.) diam. and over, a number slightly greater than that on any of the Mixed Forest plots. Even in the largest diameter class (24 in. = 61 cm. and over), the swamp plot has only slightly fewer trees (22) than the Mixed Forest plots (mean 25).

No clear-felling plots were made in the swamp forest, but the trees



Phot. 3. View from 18 ft. (24 m.) on tree in small patch of primary Mixed Rain Forest, near the Cambridge Expedition's Camp, Shasha Forest Reserve.



Phot. 4. Opening in Freshwater Swamp Akilla, Shasha Forest Reserve. The broad tree is *Mitragyna stipulosa* Ktze. (see footnote the palms are *Raphia* sp. and the large Aroic foreground is *Cyrtosperma senegalense* (Schott).



Phot. 5. Thicket of *Leea guineensis* Don in Freshwater Swamp Forest, Sample Plot 4, Shasha Forest Reserve.



Phot. 6. Freshwater Swamp Forest, edge of Sample Plot 4, Shasha Forest Reserve. The stilt-root is *Uapaca Staudtii* Pax (3416*).

appeared to be arranged in at least two strata. The higher of these, which consisted chiefly of *Mitragyna stipulosa* Ktze.,¹ *Alstonia congensis* Engl., *Lophira procera* A. Chev. and *Sarcocephalus nervosus* Hutch. & Dalz. (3407*), was probably about the same height as the second story in the Mixed Forest. The lower was formed of *Anthostema Aubryanum* Baill. (3222*), *Spondianthus* sp. cf. *ugandensis* Hutch. and many other less abundant species.

No doubt in consequence of the poor anchorage offered by the soil, trees leaning at various angles are very common. Often trees become quite horizontal and adapt themselves successfully to their new position. On the plot there were several trees of *Grewia coriacea* Mast. (3155) lying horizontally on the ground: rows of sucker shots had grown up into independent trunks and in some cases these had become completely separated from each other by the rotting of the original main trunk. Some trees of *Spondianthus* sp. cf. *ugandensis* Hutch. had been blown into a leaning position and had wrenched their roots out of the soil so as to be apparently stilt-rooted.

Buttressing is a common feature of the larger Swamp Forest trees, but the "amount of buttressing" (proportion of buttressed trees and size of their buttresses) was apparently less than in the Mixed Forest. On the other hand, stilt-rooted trees (Pl. II, phot. 6) were relatively commoner than in Mixed Forest. The frequency of buttressed and stilt-rooted trees on the Swamp plot and on two of the Mixed Forest plots is shown in the following table:

	Mixed Forest		Swamp Forest
	S.P. 2	S.P. 3	S.P. 4
Percentage of trees 4 in. (10 cm.) diameter and over with large buttresses	2.1	2.7	2.2
Do. with small buttresses	7.1	12.4	4.1
Do. with stilt-roots	1.3	1.2	7.3

The classification into "large" or "small" buttresses or stilt-roots was made according to a rough scale in the field. The most abundant of the larger trees on the swamp plot, *Mitragyna stipulosa* Ktze., is entirely without buttresses, but has remarkable knee roots: sometimes these occur as bundles of slender flexible loops, sometimes as solitary knee roots some centimetres thick.

In the swampy Mora forest in British Guiana, the dominant species had very large plank-buttresses, many of the subsidiary species were buttressed and the "amount of buttressing" was much greater than in the corresponding type of Mixed Forest (Davis & Richards, 1934, pp. 126-7). It seems from the available evidence that the "amount of buttressing" in tropical swamp forest is generally greater than in dry land forest. No reason can be suggested for the apparently abnormal condition in the Nigerian Swamp Forest.

Except for the *Leea* thickets referred to above, the *shrub layer* in the Swamp

¹ Aubréville (1936, pp. 224-6) has recently divided this species into *M. stipulosa* proper and *M. ciliata* Aubr. & Pellegr.: the former is characteristic of fringing forest in the drier inland country, the latter of the swampy coastal region from Liberia to Gaboon. The tree referred to in this paper as *M. stipulosa* will doubtless prove to belong to the second segregate.

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Forest resembles that in the Mixed Forest, though its development is less regular and the number of constituent species smaller.

Like the other layers, the *herb layer* in the Swamp Forest is exceedingly uneven in density. Generally speaking, herbs are more abundant than in the Mixed Forest: most of the species are unspecialised "shade-tolerating" plants (cf. p. 24), the "shade-loving" element is almost absent.

Climbers, both tall woody lianes and smaller herbaceous species, were considerably more abundant in the Swamp Forest than in the primary Mixed Forest, though not as abundant as in secondary forest. Many of the species present in the Mixed Forest seemed to be also present in the Swamp Forest, but some species seemed to be confined to the latter, e.g. *Mussaenda Isertiana* DC. (3202*). Among the smaller climbers, a fern, *Arthropteris obliterated* (R.Br.) J.Sm. (3244*), was very abundant. Climbing palms sometimes occur in the Swamp Forest, though they did not occur on the sample plot.

Epiphytes were also more abundant than in the Mixed Forest. The species present were similar and no species was collected in the former which was not also present in the latter. The shade community of epiphytic bryophytes (which grows more on the shrubs and young trees than on the larger trunks) is extremely abundant and rich in species. In many parts of the Swamp Forest the twigs of the undergrowth are thickly draped with *Pilotrichella communis* C.M. (3147, 3479) or another moss of pendent habit (unidentified). Epiphyllous hepaticae (*Radula* sp. or spp., Lejeuneaceae) are much more abundant in the Swamp than the Mixed Forest.

(b) *Floristic Composition*

The full results of the enumeration of trees on the sample plot are given in Table IX and some of the more important data in Tables IV and V.

The number of species is low, but both in the 4 in. (10 cm.) and over, and in the 12 in. (31 cm.) and over classes, the number is greater than on S.P. 1, the poorest of the Mixed Forest plots. In both classes it is less than on S.P. 4 and considerably less than on S.P. 3.

The floristic composition of the Swamp plot is very characteristic and differs from that of the Mixed Forest plots much more than the latter differ from one another. Out of 38 species of trees 4 in. diameter and over 27 (71 %) also occur on one or more of the Mixed Forest plots; some of these 27, however, are much commoner in the Swamp than in the Mixed Forest, viz. *Alstonia congensis* Engl., *Bridelia micrantha* Baill. (3282), *Neoboutonia glabrescens* Prain (3203) and *Grewia coriacea* Mast. (3155). Similarly some species which are abundant on all the Mixed Forest plots are represented by a few trees only on the Swamp plot, e.g. *Diospyros insculpta* Hutch. & Dalz. (90, 155 etc.). Some of the Mixed Forest species which also occur in the Swamp Forest do not reach their full size in the latter. The remaining 29 % of the species are characteristic of this type of forest and are rarely or never found except in swamps or by streams. In individuals this group forms over half the total stand and, what is even more

significant, both the most abundant species in the 4–15 in. (10–40 cm.) class (*Spondianthus* sp. cf. *ugandensis* Hutch.) and the 16 in. (41 cm.) and over class (*Mitragyna stipulosa* Ktze.) belong to it.

The latter species is so abundant as almost to deserve to be called the dominant. Though it forms only 13 % of all trees 4 in. (10 cm.) diameter and over, it forms as much as 36 % of the trees 16 in. (41 cm.) and over. It is abundant everywhere in the Fresh-water Swamp Forest of our area and the enumeration figures of the Forestry Department show that the large proportion of it present on the sample plot is not at all exceptional. In the Swamp Forest of some parts of Africa it is evidently even more decidedly dominant. According to Vermoesen (1931, p. 181), quoting from E. and M. Laurent, in the region of Lake Leopold II and the Bas-Kasaï, in the Belgian Congo, it forms pure stands, like “veritable plantations”, on the islands and low-lying flooded banks of the rivers.

The type of Fresh-water Swamp Forest represented by S.P. 2 is analogous to the swampy Mora forest of British Guiana (Davis & Richards, 1934, pp. 109–113), to which it showed considerable resemblance in aspect and general features. In two respects, however, there are important differences. First, the Mora forest had a smaller number of species of trees than any of the types of dry land forest in the same district, especially in the larger diameter classes (16 in. = 41 cm. and over), while it has just been seen that the Nigerian swamp plot is slightly richer in species than the poorest Mixed Forest plot. The reason for this difference may perhaps lie in the relative poverty in species of the Mixed Forest in the Shasha region rather than in a relatively greater richness in species of the Swamp Forest. A superficial examination of the Swamp Forest at Nikrowa suggested that it would prove very much poorer than the neighbouring Mixed Forest. The second difference is that though the Swamp Forest in both Nigeria and British Guiana shows some degree of single species dominance, in Guiana it is more complete, Mora forming 45 % of the trees 12 in. and over. Further, Mora is also the most abundant species of trees of 4–15 in. diameter, while in Nigeria *Mitragyna* falls far behind *Spondianthus* in that class. This difference illustrates the general tendency to single-species dominance shown by the Guiana forest types.

The difference in the amount of buttressing has already been referred to.

(3) THE MIXED DECIDUOUS FOREST AND ITS RELATION TO THE MIXED RAIN FOREST

As was mentioned in Section II, the Rain Forest of Nigeria at its northern limit passes into a belt of the so-called Mixed Deciduous Forest,¹ which has a drier climate, the annual rainfall being less than 1600 mm. Towards the north

¹ This section is based chiefly on information kindly supplied by officers of the Nigerian Forestry Department: the author's acquaintance with the Mixed Deciduous Forest is limited to

the igneous rocks which underlie the whole region come to the surface and it is not unlikely that the difference of soil as well as the drier climate plays a part in determining the transition from Rain Forest to Mixed Deciduous Forest. Very little, if any, of the Mixed Deciduous Forest has been completely immune from tree felling and farming, but there are some areas which probably represent the original primary forest fairly well (cf. Mackay, 1936).

MacGregor (1937, p. 236) in a recent paper considers the term "Mixed Deciduous Forest" misleading, on the ground that the Rain Forest is also a mixture of deciduous and evergreen species, though in different proportions. Though this is true, it is difficult to suggest a better name. It is probably not desirable to use the name "Monsoon Forest" for the West African Mixed Deciduous Forests as they do not seem to correspond in all respects to the Monsoon Forests of India and Burma. Outside Africa the most nearly analogous types would seem to be the "Southern Tropical Semi-Evergreen" Forest of India and Burma (Champion, 1936) and the "Semi-Deciduous" Forest of Trinidad (Marshall, 1934, p. 41).

In structure the Mixed Deciduous Forest shows a general resemblance to Rain Forest. The trees are arranged in more than one story. The upper tree stories are less dense and their average height is perhaps lower than in the Rain Forest.² The most important difference from the Rain Forest is, of course, the larger proportion of trees deciduous in the dry season, but evergreen species are so numerous that even at the height of the dry season the forest does not have the leafless appearance of a temperate deciduous forest in winter. The shrub and lowest tree stories are entirely evergreen. Lianes are frequent, but, as might be expected from the relatively dry climate, epiphytes are few in both species and individuals. The only common epiphyte is a *Platyserium* (probably *P. stemaria* (Beauv.) Desv.).

The commonest of the larger species of trees are *Arere*, *Triplochiton scleroxylon* K. Schum., *Aye*, *Sterculia rhinopetala* K. Schum., *Ita*, *Celtis* spp., *Itako*, *Strombosia* sp., *Ofun*, *Mansonia altissima* A. Chev., *Omodon*, *Ricino-dendron africanum* Muell. Arg., *Oporoporo dudu*, *Cola cordifolia* (Cav.) R.Br., *Otutu*, *Cistanthera papavifera* A. Chev. etc. Most of these are species which are either uncommon in the Rain Forest or quite absent. *Triplochiton* is often very abundant: in one mile of enumeration line in the northern Shasha Reserve it formed 20 % of all trees 4 ft. (1.22 m.) girth and over (= 15 in. or 38 cm. diam.). While many common rain-forest species are almost equally common in the

short visits to the doubtfully primary forest at Olokemeji and the much modified Mamu Reserve. The data on floristic composition are taken from the results of the Forestry Department's enumeration surveys in the Akure and Shasha Reserves. These enumerations were made by vernacular names on belt transects 1 chain (20.1 m.) wide and 100 chains (2012 m.) apart. The botanical equivalents of the names were also provided by the Forestry Department.

¹ Burt Davy (1938, p. 33) suggests "Tropical Semi-evergreen forest."

² Since Rain Forest species may penetrate northwards into the Mixed Deciduous Zone along streams, etc., it is difficult to be sure from the available data which Rain Forest species are absent from typical Mixed Deciduous Forest.

Mixed Deciduous Forest, others are entirely absent, e.g. *Casearia bridelioides* Mildbr. ex Hutch. & Dalz., *Lophira procera* A. Chev. Some common Mixed Deciduous species are found chiefly in secondary forest in the Rain Forest Zone, e.g. *Terminalia superba* Engl. & Diels: this may be because they are intolerant of deep shade.

The Forestry Department's enumeration figures for the Shasha Reserve show that the transition from Rain Forest to Mixed Deciduous Forest is gradual. The presence of characteristic Mixed Deciduous species and the absence of characteristic rain-forest species only becomes marked in the extreme north of the Reserve.

A type of forest similar to the Mixed Deciduous Forest apparently forms a belt from French Guinea in the west, with some interruptions, to Nigeria and probably on into the Congo basin. Different authors have taken different views as to its status. Mildbraed does not recognize it as a distinct type from the Rain Forest, as he says: "In Africa, at any rate, north of the Equator, the Rain Forest, though somewhat impoverished in composition and in its general character, abuts directly on the southern Sudanese *Laubsavanne* (savannah without thorn trees)" (1922, p. 46, transl.). On the Gold Coast what is evidently a very similar type of vegetation to the Mixed Deciduous Forest is described by Chipp (1927) as the "Triplochiton-Piptadenia Preclimax" and is regarded as one of the "units" of the "Monsoon Climax", which also includes types of Rain Forest. As the difference between the Mixed Deciduous and the Rain Forest is certainly mainly dependent on a difference in the *general* climate, this treatment does not seem logical.

In view of the wide distribution of the Mixed Deciduous Forest and its considerable differences in floristic composition from the Rain Forest, it has some claim to be regarded as an independent climatic climax, but more knowledge of it is needed before it can be definitely ranked as such.

VI. CONCLUSIONS

A comparison between the Rain Forest of south-western Nigeria and that previously studied by the author in British Guiana and Sarawak shows that, within a strong general resemblance in structure and floristic make-up, there are some important differences. The chief of these may be briefly recapitulated:

- (1) The considerably more open first (top) and second tree stories of the Nigerian forest. No doubt closely connected with this is the larger proportion of the third-story trees which are true third-story species and not young trees of first- and second-story species.

- (2) The relative floristic poverty of the Nigerian forest. This is a feature not only of all three tree stories, but also of the shrub and herb layers and of the climbers and epiphytes.

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Other minor, but possibly significant, differences are the apparently more marked seasonal periodicity of the undergrowth, the scarcity of cauliflorous trees, the absence or scarcity of saprophytic flowering plants, and the fact that the Swamp Forest trees were not more buttressed than those of the Mixed Forest. In respect of single-species dominance, the Nigerian forest is intermediate between British Guiana and Sarawak, the tendency to dominance being about equal to that in Guiana in the Mixed Forest and considerably less than in the comparable type of forest in Guiana in the Fresh-water Swamp Forest.

At present it is impossible to say how many of these differences represent widespread characteristics of the African Rain Forest and how many represent local peculiarities of the region. It seems quite likely, however, that some of the features of the Nigerian forest are not general African characteristics, but are local features depending on the fact that south-western Nigeria is close to the climatic limit of Rain Forest.

The first of the major differences—the open first and second tree stories—may quite possibly be connected with the relatively unfavourable climate, though it is impossible to exclude human interference as a possible cause. The severe dry season is almost certainly the cause of some of the minor differences between the Nigerian forest and that of Guiana and Sarawak.

The floristic poverty of the Nigerian forest—the second of the major differences—can only be attributed partly to the unfavourable climate, as there is good evidence that relative floristic poverty is a characteristic of the African Rain Forest in general. Jentsch's Plot V in the Cameroons is, it is true, richer than either the Guiana or the Borneo plots (considering trees 16 in. diam. and over, the only available basis of comparison), but it is generally admitted that the Cameroons is one of the richest regions of the African Rain Forest and is probably to be regarded as the chief centre of evolution of the Rain Forest flora. Taking the flora of the African Rain Forest as a whole, there is no doubt as to its smallness compared with that of either the South American or the Asiatic Rain Forest.

Closely connected with its comparative poverty is its remarkable uniformity, a subject which has been discussed by Mildbraed (1914, pp. 688–90 and 1922, pp. 101–3). He points out that there is a marked absence of local endemism and that localities far apart often have a very similar flora. Neighbouring localities differing in relief and climate often differ more in their flora than similar localities separated by great distances. This uniformity of the African flora Mildbraed attributes to the great climatic changes the region has suffered in the past: these have caused great migrations of floras and levelled local peculiarities. If this is so, it is easy to understand why regions on the extreme edge of the Rain Forest area, such as south-western Nigeria, should show a very marked poverty in species.

VII. SUMMARY

1. The Rain Forest of south-western Nigeria was examined with the chief object of comparing it with Rain Forest in British Guiana and Sarawak previously studied by the author.

2. Originally it formed a belt parallel to the coast lying between a belt of lagoons and swamps of the seaward side and a belt of Mixed Deciduous Forest on the inland side.

3. Owing to the development of agriculture, the continuous belt of forest has been converted into isolated blocks, most of which are now set apart as forest reserves. Most of the forest within these reserves is secondary or heavily depleted and timber exploitation is still being carried on in them. Small relict areas still exist, however, in which some trees may have been felled in the past, but which probably represent fairly accurately the original primary forest of the region. An intensive study was made of some of these relict areas in the Shasha and Okomu Forest Reserves.

4. The Rain Forest of the whole of south-western Nigeria is situated near its climatic limits. The annual rainfall varies from over 2600 mm. to just over 1600 mm., but the dry season is strongly marked, 2-5 consecutive months have less than 50 mm. Where the annual rainfall falls below 1600 mm., the Rain Forest gives place to Mixed Deciduous Forest, but the annual rainfall is not believed to be the factor directly responsible for the boundary between the two.

5. Only two types of primary Rain Forest were met with, the Mixed Rain Forest and the Fresh-water Swamp Forest. The former is considered to be the climatic climax of the region and the latter an edaphic climax conditioned by a high-water table.

6. A number of soil profiles in primary Mixed Rain Forest are described: these soils belong to the Tropical Red Earth or Yellow Earth types.

7. The stratification of the Mixed Forest is described with the help of profile diagrams. There are three fairly well-defined stories of trees at 120-150 ft. (37-46 m.), 50-120 ft. (15-37 m.) and up to 50 ft. respectively. Beneath the tree stories there are ill-defined shrub and herb strata. The herb stratum is composed of synusiae of shade-loving and shade-tolerating species: the latter are analogous to the "wood marginal" species of temperate woodlands.

8. The synusiae of climbers and epiphytes are described. The epiphytic vegetation of the region is remarkably poor in species.

9. The floristic composition of the Mixed Forest was studied by enumerating according to their vernacular names all trees of 4 in. (10 cm.) diameter and over on sample plots each 160,000 sq. ft. (1.49 ha.) in area. Two plots were situated in the Shasha Reserve and one in the Okomu Reserve. By careful collecting the botanical equivalents of a large proportion of the vernacular names were obtained. On all three plots there is a mixture of species without marked dominance of any one species, though on one plot a single species

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formed as much as 35 % of all trees 16 in. (41 cm.) diameter and over. The number of tree species per plot is relatively small, viz. 34–70. The composition differs considerably on the three plots, each representing what are probably different facies of the same association.

10. An account is given of the soil and structure of an area of Fresh-water Swamp Forest in the valley of a small stream. In structure this type of forest differs from the Mixed Forest chiefly in its greater irregularity.

11. On a sample plot of Fresh-water Swamp Forest the number of species present was small, though actually greater than on the poorest of the Mixed Forest plots. 36 % of trees of 16 in. (41 cm.) diameter and over belonged to a species of *Mitragyna*: the majority of the subsidiary species also occurred in the Mixed Forest, but the remainder were confined to Swamp Forest.

12. Some remarks are made on the distribution and chief characteristics of the Mixed Deciduous Forest and the question of its status is touched on.

13. The chief differences between the Rain Forest of south-western Nigeria and that of British Guiana and Sarawak are reviewed and briefly discussed.

REFERENCES

- Ainslie, J. R.** "The physiography of Southern Nigeria and its effect on the forest flora of the country." *Oxford For. Mem.* **5**, 1926.
Annual Report of the Forest Administration of Nigeria, Lagos, 1930.
- Aubréville, A.** "La forêt de la Côte d'Ivoire." *Bull. Com. A.O.F.* **15**, 205–61, 1933.
- Aubréville, A.** *La flore forestière de la Côte d'Ivoire*. 3 vols. Paris, 1936.
- Brooks, C. P. E.** "The rainfall of Nigeria and the Gold Coast." *Q.J. Roy. Met. Soc.* **42**, 85–106, 1916.
- Brooks, C. P. E.** "The distribution of temperature over Nigeria." *Q.J. Roy. Met. Soc.* **46**, 204–14, 1920 a.
- Brooks, C. P. E.** "The distribution of relative humidity over Nigeria." *Q.J. Roy. Met. Soc.* **46**, 289–92, 1920 b.
- Brunthaler, J.** "Vegetationsbilder aus Deutsch-Ostafrika. Regenwald von Usambara." *Vegetationsbilder*, **11**, 8, 1914.
- Burt Davy, J.** "The classification of tropical woody vegetation types." *Imp. For. Inst. Paper*, **13**, 1938.
- Campbell, W. J. F.** "Some problems in soil morphology." MS. Thesis for B.Sc. degree, University of Oxford, 1936.
- Champion, H. G.** "A preliminary survey of the forest types of India and Burma." *Ind. For. Rec.* N.S. **1**, 1–286 + i–x and i–viii, 1936.
- Chevalier A.** *Les végétaux utiles de l'Afrique tropicale. IX. La forêt et les bois du Gabon*. Paris, 1917.
- Chipp, T. F.** "The Gold Coast forest. A study in synecology." *Oxford For. Mem.* **7**, 1927.
- Davis, T. A. W. & Richards, P. W.** "The vegetation of Moraballi Creek, British Guiana: an ecological study of a limited area of tropical rain forest." Part I, *This JOURN.* **21**, 350–84, 1933; Part II, *This JOURN.* **22**, 106–55, 1934.
- Engler, A.** *Die Vegetation der Erde. IX. Die Pflanzenwelt Afrikas*. **1**, 2te Hälfte, Leipzig, 1910., London, 1931; vol. **2**, pt. II, London, 1936.
- Jentsch.** "Der Urwald Kameruns. Folgerungen aus den auf der Expedition 1908/09 gewonnenen Erfahrungen in Bezug auf den Zustand und die Nutzbarmachung des Waldes." *Beih. Tropenpflanzer*, **12**, 1–199, 1911.
- Kennedy, J. D.** *Forest flora of Southern Nigeria*. Lagos, 1936.

- MacGregor, W. D.** "Forest types and succession in Nigeria." *Emp. For. J.* **16**, 234-42, 1937.
- Mackay, J. H.** "Problems of ecology in Nigeria." *Emp. For. J.* **15**, 190-200, 1936.
- Marshall, R. C.** "The physiography and vegetation of Trinidad and Tobago." *Oxford For. Mem.* **17**, 1934.
- Mildbraed, J.** "Die Vegetationsverhältnisse im Sammelgebiet der Expedition." *Wiss. Ergebn. dtsch. Zentral-Afrika-Expedition 1907-1908*, **2** (Botanik), Leipzig, 1914.
- Mildbraed, J.** *Wissenschaftliche Ergebnisse der Zweiten Deutschen Zentral Afrika-Expedition 1910-1911, unter Führung Adolf Friedrichs, Herzog zu Mecklenburg*, **2** (Botanik), Leipzig, 1922.
- Mildbraed, J.** "Probeflächen-Aufnahmen aus dem Kameruner Regenwald." *Notizbl. Bot. Gart. Berlin-Dahlem*, **10**, 951-76, 1930 a.
- Mildbraed, J.** "Zusammensetzung der Bestände und Verjüngung im tropischen Regenwald." *Ber. dtsch. bot. Ges.* **48**, Generalversammlungsheft, 50-7, 1930 b.
- Mildbraed, J.** "Ein Hektar Regenwald auf Fernando Poo, aufgenommen von H. Burekhardt." *Notizbl. Bot. Gart. Berlin-Dahlem*, **11**, 946-50, 1933.
- Nigeria Handbook*, 10th edition, Lagos, 1933.
- Richards, P. W.** "Ecological observations on the rain forest of Mount Dulit, Sarawak. Part I." *This Journ.* **24**, 1-37, 1936.
- Salisbury, E. J.** "The structure of woodlands." *Festschr. C. Schroeter*, 334-54, Zürich, 1925.
- Sykes, R. A.** "Some notes on the Benin forests of Southern Nigeria." *Emp. For. J.* **9**, 101-6, 1930.
- Vermoesen, C.** *Les essences forestières du Congo Belge. I. Manuel des essences de la région équatoriale et du Mayombe*. Brussels, 1931.

Note to Tables VI-IX

In these tables the following conventions are used to indicate the degree of reliability of the botanical equivalents of the vernacular names:

1. Botanical names not in italics are taken from a list of equivalents of vernacular names kindly provided by the Conservator of Forests, Ondo Circle. These can be used for species on the sample plots only with caution, as the material on which they are based was not necessarily collected in the same district, but they are only quoted when there is a fair probability of their correctness.

2. Botanical names in italics are based on observations by members of the Cambridge Expedition: as in the text, names followed by collector's numbers are based on material collected, names without numbers are identifications made in the field with the help of the *Flora of West Tropical Africa*. Numbers with an asterisk indicate that the specimen was collected on the sample plot in question.

3. ? before a name indicates doubt as to the identity of the species on the plot and the specimen collected: ? after a name indicates doubt as to the correct identification of the specimens collected.

Table VI. Sample Plot 1. Mixed Primary Rain Forest
About 8 km. north of Akilla, Shasha Forest Reserve (Ijebu Province)

Vernacular name	Species	Diameter class						Total no. of individuals 4 in. (10 cm.) diameter and over	Total no. of individuals 16 in. (41 cm.) diameter and over
		4-7 in. (10-19 cm.)	8-11 in. (20-29 cm.)	12-15 in. (30-40 cm.)	16-19 in. (41-50 cm.)	20-23 in. (51-60 cm.)	24 in. and over (61 cm. and over)		
Aba	<i>Ficus</i> sp. ("Strangling" fig)	3	—	—	—	1	1	2	—
Agba Irosun	<i>Baphia pubescens</i> Hook. f. (3006)	—	—	—	—	—	—	3	—
Agbawu	<i>Musanga Smithii</i> R. Br.	7	3	—	—	—	—	10	—
Ajeleru	<i>Canthium glaberrimum</i> (K. Schum.) Hiern (129, 187)	—	—	1	1	—	—	2	1
Akilla	<i>Isolona</i> n.sp. ? aff. <i>campanulata</i> Engl. & Diels (3343)	—	1	1	—	—	1	3	1
Akome (? = Ako)	? <i>Octolobus angustatus</i> Hutch. (3115)	1	—	—	—	—	—	1	—
Omeyin									
Akomu	<i>Prenanthus Kombo</i> Warb.	1	—	—	—	—	—	1	—
Apado	<i>Berlinia auriculata</i> Bth. (3158*, 3406, 3487*)	5	5	3	5	5	12	35	22
Asofeje	<i>Rauwolfia vomitoria</i> Afz. (3333*)	1	—	—	—	—	—	1	—
Atole	<i>Sapium ellipticum</i> (Hochst.) Pax (250)	1	1	—	—	1	1	4	2
Awasa Odida	<i>Macaranga Barteri</i> Muell. Arg. (3246)	—	1	—	—	—	—	1	—
Aye	<i>Sterculia rhinopetala</i> K. Schum. (31, 61)	—	1	—	—	—	—	1	—
Ebo	<i>Casuaria briddingtonii</i> Mildbr. ex Hutch. & Dalz. (69, 3046, 3302, 3370, 3374)	2	3	1	1	—	2	9	3
Egunun Ibo									
Epowu	<i>Neoboutonia glabrescens</i> Prain (3203)	1	1	—	—	—	—	1	—
Erin	<i>Pteridroma umbellata</i> (Stapf) Stapf (8, 142, 3162*, 3211)	9	15	6	—	—	—	30	—
Erin	<i>Euglyptophloeum microanthum</i> Harms (3376, 3453)	—	—	—	2	—	2	2	2
Egununapon	<i>Diospyros confertiflora</i> Gürke (191, 3161*, 3443)	20	19	12	6	1	1	58	7
Idagbon, Abo	Under these names are included one or more of the following:	8	7	5	1	—	1	22	2
Idagbon, Ako	<i>Corynanthe pachyceras</i> K. Schum. (3075)	2	1	—	—	—	—	3	—
	<i>Pausingstata brachythyrsa</i> De Wild. (67, 3047)								
	<i>P. Taihotii</i> Wernh. (240, 3356), and possibly other spp. of <i>Pausingstata</i>								
Idapopo	<i>Conopharyngia penduliflora</i> Stapf (9, 3076, 3332*)	28	—	—	—	—	—	28	—
Igi Dudu	<i>Diospyros</i> sp. (several species included under this name)	—	1	—	—	—	—	1	—
Itako	<i>Strombosia pustulata</i> Oliv. (3428, 3444) (and other spp. of <i>Strombosia</i> ?)	4	3	2	—	—	—	9	—

Odoko	14	14	13	6	6	4	57	16
<i>Scottellia kamerunensis</i> Gilg (15, 78, 125, 194, 234, 277, 343, 3452) and/or n.sp. (161, 3432)								
Ogwagwa or Keso	6	2	2	—	—	—	10	—
<i>Diospyros chrysantha</i> Gürke (72, 3213, 3331)							1	—
Ologbotyin	49	7	—	—	—	—	56	—
Ombé								
<i>Rinorea</i> sp. cf. <i>oblongifolia</i> (C. H. Wright) Marquand (242, 3156*, various spp. of <i>Rinorea</i> included under this name, but probably only one on plots)								
Ombé, Ako	1	—	—	—	—	—	1	—
Opalifon	3	5	2	—	—	—	10	—
<i>Xylopia Quintarii</i> Engl. & Diels (68, 3159*, 3334*, 3434)								
Ora Igbo	1	1	—	—	—	—	2	—
<i>Conopharyngia pachysiphon</i> Stapf (167)							1	—
Orririka	153	59	15	2	—	—	229	2
Oshun								
<i>Diospyros insculpta</i> Hutch. & Dalz. (90, 155, 186, 3480*, 3486*)								
Otorotara	1	—	1	2	—	—	4	2
<i>Grewia coriacea</i> Mast. (3155)							7	—
Telefon or Igbaika	7	—	—	—	—	—	—	—
<i>Casaria</i> n.sp. (3081, 3151, 3191)								
	329	150	64	25	14	24	606	63

II. Shrubs and herbs

(a) Shrubs

<i>Anglocalyx oligophyllus</i> Bak. f. (23, 3069)	r.	
<i>Carpodina alba</i> Don (3443*)	v.r.?	
<i>Craterispermum cerinanthum</i> Hiern (3382)	v.r.?	
<i>Dicranolepis grandiflora</i> Engl. (3188*, 3199) and <i>D. stenophora</i> H. H. W. Pearson (3015, 3150*, 3207)	o.	
<i>Dracaena surculosa</i> Lindl. (5)	r.	
<i>Icacina trichantha</i> Oliv. (3142* etc.)	f.	
<i>Icacina</i> sp.?	f.	
<i>Mimicylon membranifolium</i> Hook. f. (3179*, 3305)	r.	
<i>Ouratea Oliveriana</i> Gilg (3210, 3330*)	a.	
<i>Oxyanthus tenuis</i> Stapf (3217, 3351*)	v.r.?	
<i>Psychotria sciadaphora</i> Hiern (3183*)	v.r.?	
<i>Rinorea</i> sp. (3171*, prob. = 3303 on S.P. 3)	l.f.	
<i>Rinorea</i> sp. (3172*, prob. = 3232 on S.P. 4)	v.a.-l.f.	
<i>Sphenocentrum Jollyanum</i> Pierre (3306)	o.	
	v.r.?	

(b) Herbs (excluding epiphytes)

(i) Dicotyledons:	
<i>Geophila cordiformis</i> A. Chev. (3187*, 3403)	r.
<i>G. hirsuta</i> Bth. (3167*, 3180*, 3304, 3384, 3402)	l.a.
<i>Lankasteria Barteri</i> Hook. f. (3021)	l.a.
<i>L. myrsoides</i> S. Moore (48, 3017)	r.

Pseudanthephium tunicatum (Afz.) Milne-Redhead (258, 3071, 3102, 3175*)

<i>Psychotria</i> sp. (3168*)	v.r.	(in opening)
Rubiaceae (or tree seedling?)	f.	
<i>Thomningia sanguinea</i> Vahl (3011, 3421)	r.	

(ii) Monocotyledons:

Araceae (probably normally epiphytic)	r.	
<i>Burfordia imperforata</i> C. B. Clarke (3177*, 3228, 3306)	r.	
<i>Dracaena phrynioides</i> Hook. (228)	r.	
<i>Heteraria Stammleri</i> (Schlecht.) Summerh. (3072)	v.r.	
<i>Leptaspis cochlearia</i> Thw. (3182*, 3208)	f.-l.a.	
<i>Nephthytis coarctata</i> N. E. Br. (3154*, 3379)	o.	
<i>Palisota ambigua</i> (Beauv.) C. B. Clarke (3141*)	o.-f.	
<i>P. Barteri</i> Hook. f. (53, 3184*, 3339)	o.-f.	
<i>Polyspatha paniculata</i> Bth. (3173*)	r. (openings)	

(iii) Ferns:

<i>Dryopteris protensa</i> (Afz.) C. Chr. (3109*, 3306)	r.	
? <i>Lomariopsis palustris</i> (Hook.) Alston (3239, 3418)	o.?	
<i>Nephrolepis biserrata</i> (Sw.) Schott (3170*, 3386)	l.f. (opening)	
<i>Pteris atroviensis</i> Willd. (3180*)	o.	

Table VII. *Sample Plot 2. Mixed Primary Rain Forest*
Near Eluju village, about 5 km. north of Akilla, Shasha Forest Reserve (Ijebu Province)

I. Trees 4 in. (10 cm.) diameter and over										
Op. = found chiefly or entirely near openings										
Vernacular name	Species	Diameter class						Total no. of individuals 4 in. (10 cm.) diameter and over	Total no. of individuals 16 in. (41 cm.) diameter and over	
		4-7 in. (10-19 cm.)	8-11 in. (20-29 cm.)	12-15 in. (30-40 cm.)	16-19 in. (41-50 cm.)	20-23 in. (51-60 cm.)	24 in. (61 cm. and over)			
Aghawu	<i>Musanga Smithii</i> R.Br.	4	1	1	2	—	—	5	2	
Ajeleru	<i>Canthium glaberrimum</i> (K. Schum.) Hiern (129, 187)	3	1	—	—	—	—	1 (Op.)	—	
Akila	<i>Isolona n.sp.</i> ? aff. <i>capitulata</i> Engl. & Diels (3343)	—	—	—	—	—	—	—	—	
Apako	Annonaceae	—	—	—	—	—	—	—	—	
Arumo	—	1	—	—	—	—	—	—	—	
Ata	<i>Fagara macrophylla</i> (Oliv.) Engl. (3433)	1	—	—	—	—	—	2	1	
Atole	<i>Sapium ellipticum</i> (Hochst.) Pax (250)	—	1	—	—	—	—	1	—	
Awasa Odida	<i>Macaranga Barteri</i> Muell. Arg. (3246)	1	—	—	1	—	—	1 (Op.)	—	
Awetiwei	<i>Mayrunea membranacea</i> Pax & K. Hoffm. (188)	1	—	1	—	—	—	3	2	
Ayewoso	—	1	—	—	—	—	—	2 (Op.)	—	
Aye	<i>Sterculia rhinopodala</i> K. Schum. (31, 61)	2	—	—	—	—	—	1	—	
Ayenyen Igbo	—	1	—	—	—	—	—	2	—	
Ebo	<i>Casuarina brideloides</i> Mildbr. ex Hutch. & Dalz. (69, 3046, 3302, 3370*, 3374)	43	22	10	9	4	2	90	15	
Ekki	<i>Lophira procera</i> A. Chev.	—	—	—	—	—	—	—	—	
Epupa Iroko	<i>Rinorea</i> sp. cf. <i>dentata</i> (Beauv.) Ktze. (58, 113, 3426*). (More than one sp. included under this name, but probably only one on this plot.)	7	—	—	1	—	2	3	—	
Erikesi	<i>Diospyros mombutensis</i> Gurke (18, 3204, 3329)	1	—	—	—	—	—	1	—	
Erin	<i>Picralima umbellata</i> (Stapf) Stapf (8, 142, 3162, 3211)	4	5	2	2	—	—	13	2	
Esununapon	<i>Erythrophloeum microanthum</i> Harms (3376*, 3453*)	—	—	—	—	—	—	13	13	
Idagbon, Abo	<i>Diospyros confertiflora</i> Gurke (191, 3161, 3443*)	10	21	18	3	4	2	58	9	
Idagbon, Ako	Under these names are included one or more of the following: <i>Corynanthe pachytera</i> K. Schum. (3075) <i>Pausinystalia brachyhyrsa</i> De Wild. (67, 3047) <i>P. Talbotii</i> Wernh. (240, 3356), and possibly other spp. of <i>Pausinystalia</i>	2	—	1	—	1	1	5	2	
Itako	<i>Strombosia pustulata</i> Oliv. (3428*, 3444*) (and other species of <i>Strombosia</i> ?)	2	—	2	—	—	—	4	—	
Jesebe or Akika	<i>Disoclyptrenna caloneura</i> (Pax) Prain (3221, 3340)	49	55	18	5	—	—	127	5	
Agha	<i>Homalium dolichophyllum</i> Gilg (3123) (or <i>H. africanum</i> Bth. (3321)?)	4	1	—	—	1	1	7	2	
Kalado	—	1	—	—	—	—	—	1	—	
Lapawe	—	—	—	—	—	—	—	—	—	
Laposara	—	1	1	—	—	—	—	2	—	
Odoko	<i>Scottellia kamerunensis</i> Gilg (15, 78, 125, 194, 234, 3271, 3431*, 3452*) and/or n.sp. (161, 3432*)	19	7	7	4	3	1	41	8	
Ofuye	Guarea Thompsonii Sprague & Hutch.	2	—	—	—	—	—	2	—	

I. Trees 4 in. (10 cm.) diameter and over
Op. = found chiefly or entirely near openings

Ogwagwa or Keso	<i>Diospyros chrysantha</i> Gürke (72, 3213, 3331)	4	12	4	—	—	20
Ojojo Ormode	<i>Mareya micrantha</i> Muell. Arg. (157, 3193)	1	—	—	—	—	1 (Op.)
Kotale	—	—	—	—	—	—	—
Okarakara	—	—	—	—	—	—	—
Olepo	—	4	—	1	1	—	6 (Op.)
Oloka	—	2	—	—	—	—	2
Ombe	? <i>Garcinia ovalifolia</i> Oliv. (154) <i>Rinorea</i> sp. cf. <i>oblongifolia</i> (C. H. Wright) Mar- quand (242, 3156. Various spp. of <i>Rinorea</i> included under this name, but only one on plots)	100	40	4	—	—	153
Ombe, Ako	—	6	—	—	—	—	6
Opalifon	<i>Xylopia Quintassi</i> Engl. & Diels (68, 3159, 3334, 3434*)	10	2	—	—	—	12
Opepe	<i>Sarcocaphalus Diderrichii</i> De Wild (3276)	1	1	1	2	—	4
Osho Pupa	<i>Evantia chlorantha</i> Oliv.	1	—	—	—	—	7
Oshun	<i>Diospyros inaequalis</i> Hutch. and Dalz. (90, 155, 186, 3480, 3486)	78	17	1	—	—	96
Osiri	<i>Mencylon cinnamomoides</i> Gilg (241*) (and other species of <i>Mencylon</i> ?)	1	1	1	—	—	3
Sapo Sapo	<i>Autocleista Vogeltii</i> Planch. or <i>A. nobilis</i> G. Don	—	—	—	1	—	1 (Op.)
Shekarajo	—	54	—	—	—	—	2
Telefon or Igbaika	<i>Casaria</i> n.sp. (3061, 3157, 3191)	440	196	74	32	13	54
							781

II. Shrubs and herbs

<i>Angelicocalyx oligophyllus</i> Bak. f. (23, 3069)				<i>Psychotria</i> sp. (3365* prob. = 3307 on S.P. 3)			
<i>Craterispermum cerinthanthum</i> Hiern (3382)				<i>Psychotria</i> sp. (3381*)			
<i>Dicranolepis grandiflora</i> Engl. (3188, 3199) and/or <i>D. stenosiphon</i>				Rubiaceae l.			
H. H. W. Pearson (3015, 3150, 3207)				Rubiaceae II (? tree seedling)			
<i>Dracaena surculosa</i> Lindl. (5)				<i>Thonningia sanguinea</i> Vahl (3011, 3421*)			
<i>Hesperia</i> sp. cf. <i>parvifolia</i> Sm. (3419*)				(ii) Monocotyledons:			
<i>Iaccina trichantha</i> Oliv. (3142 etc.)				<i>Anchomanes</i> sp.			
<i>Mencylon</i> sp. (3397*)				Araceae			
<i>Mencylon</i> sp. (3398*)				<i>Bufoerestia imperforata</i> C. B. Clarke (3177, 3228, 3336*)			
<i>Mencylon</i> sp. (3400*)				<i>Costus Englerianus</i> K. Schum. (3396*)			
<i>Ouratea Kulsoni</i> De Wild. (3420*)				<i>Dracaena phrynioides</i> Hook. (228)			
<i>Ouratea</i> sp. aff. <i>myriconeura</i> Gilg (3371*)				<i>Harmanthus cinnabarinus</i> Decne. (3079, 3417)			
<i>Psychotria tenuis</i> Stapf (3217, 3354)				<i>Leptaspis cochleata</i> Thw. (3182, 3208)			
<i>Raphia</i> sp. (young)				<i>Verhulstia constricta</i> N. E. Br. (3154, 3379*)			
<i>Sphenocentrum</i> sp. cf. <i>Jollyanum</i> Pierre (3306)				<i>Pachista ambigua</i> (Beaut.) C. B. Clarke (3141)			
				<i>P. Barteri</i> Hook. f. (53, 3184, 3336)			
				<i>Pollia condensata</i> C. B. Clarke (3391*)			
				<i>Polyspatha paniculata</i> Bth. (3176)			
				(iii) Ferns:			
				<i>Adiantum Vogeltii</i> Mett. (3235, 3386*)			
				<i>Bolbitis auriculata</i> (Sw.) Alston (3242, 3316, 3383*)			
				<i>Dryopteris dentata</i> (Forsk.) C. Chr. var. (3392*)			
				<i>D. protensa</i> (Alf.) C. Chr. (3169, 3306)			
				<i>Microlepia sphenocaulae</i> (L.) T. Moore (3383*)			
				<i>Nephrolepis biserrata</i> (Sw.) Schott (3170, 3388*)			
				<i>Pteris</i> n.sp. (3387*)			

(i) Dicotyledons:

- Geophila condiformis* A. Chev. (3187, 3408*)
G. hiruta Bth. (3167, 3166, 3304, 3381*, 3402*)
G. ovalata F. Ditr. (3401*)
Lankasteria thyrsoidea S. Moore (46, 3017)
Leea sp. (not *L. guineensis* Don) (3064)

(b) Herbs (excluding epiphytes)

- l.f.*
l.f. (v.a. in openings)
l.f. (a. in openings)
o. (f. in openings)
o. (only in openings)

- o.*
f.-o. (f. in openings)
v.r.
o.
v.r. (openings only)
v.r.? (openings only)
r. (f. in openings)
l.a.
o.
v.r.
f.-l.a. (a. in openings)
o.-f.
o. (f. in openings)
f.
r. (openings only)
v.r.

Table VIII. *Sample Plot 3. Mixed Primary Rain Forest*
About 6 km. north of Nikrowa Camp, Okomu Forest Reserve (Benin Province)

Vernacular name	Species	Diameter class						Total no. of individuals 4 in. (10 cm.) diameter and over	Total no. of individuals 16 in. (41 cm.) diameter and over
		4-7 in. (10-19 cm.)	8-11 in. (20-29 cm.)	12-15 in. (30-40 cm.)	16-19 in. (41-50 cm.)	20-23 in. (51-60 cm.)	24 in. and over (61 cm. and over)		
Afara	<i>Terminalia superba</i> Engl. & Diels (3040)	5	1	—	—	—	—	—	1
Agba Irosun	<i>Baphia pubescens</i> Hook. f. (3006)	—	—	1	—	—	—	—	6
Agbawu	<i>Musanga Smithii</i> R.Br.	—	2	—	1	—	—	—	3
Agomo	—	—	—	—	—	—	6	—	6
Ahun	<i>Alstonia congensis</i> Engl.	3	—	—	—	—	—	—	3
Akabairu	—	—	—	—	—	—	—	—	—
Angwin	—	1	—	—	—	—	—	—	—
Apako	—	7	2	3	1	—	2	1	15
Areke	<i>Amonaceae</i>	1	—	—	—	—	—	—	1
Arere	<i>Triplachton scleroxylon</i> K. Schum. (134)	—	—	—	—	—	—	—	1
Arumo	—	4	1	—	—	—	—	—	5
Asofeyeje	<i>Rauvolfia vomitoria</i> Afz. (3333)	2	—	—	—	—	—	—	2
Ata	<i>Fagara</i> sp.	—	—	—	—	—	—	—	—
Atinushigon	<i>Hylocicodon gabunensis</i> Taub.	1	2	—	1	—	—	—	1
Atole	<i>Scaphium ellipticum</i> (Hochst.) Pax (250)	8	—	5	2	—	—	—	3
Awasa Angba	<i>Bridelia mitrantha</i> Baill. (3282)	—	1	—	—	1	—	—	18
Awasa Otida	<i>Macaranga Barteri</i> Muell. Arg. (3246)	1	—	—	—	—	—	—	1
Aworoso	—	—	4	—	1	—	—	—	1
Ayan, Ako	? <i>Alizia bella</i> Harms	5	1	1	—	—	—	1	5
Ayan Olutoko	<i>A. bipindensis</i> Harms (25)	3	—	—	—	—	—	—	2
Buje	<i>Randia</i> sp. or near	1	—	—	—	—	—	1	3
Ebo	<i>Casuarina pyramidalis</i> Millbr. ex Hutch. & Dalz. (69, 3046, 3302*, 3370, 3374)	—	—	—	—	—	—	—	1
Egbeni	—	1	—	—	1	—	—	—	1
Ekanhoho (B)	<i>Lophira procera</i> A. Chev.	—	—	—	—	—	—	—	1
Eki	<i>Pentameria umbellata</i> (Stapf) Stapf (8, 142, 3162, 3211)	1	3	1	1	—	2	—	3
Erin	<i>Erythrophloeum</i> Harms (3376, 3455)	—	—	—	—	—	—	—	6
Erin	<i>Disopyrus confertiflorus</i> Gürke (191, 3161, 3443)	7	8	14	4	1	2	—	3
Esumunapon	<i>Diospyros purpurea</i> Gürke (168)	4	6	1	—	—	—	—	35
Esumunapon	(3301*)	2	—	—	—	—	—	—	11
Eyegbo (B)	? <i>Pachylobus balsamifer</i> (Oliv.) Gaillaud.	4	1	1	—	—	—	—	2
Eyegbo (B)	<i>Pausanystalia brachytricha</i> De Wild. (67, 3047), and/or	4	6	4	7	2	1	—	6
Idagbon, Abo	<i>P. talbotii</i> Wernh. (240, 3356) (may also include species of <i>Pachystylia</i>)	—	—	—	—	—	—	—	24
Idagbon, Abo	<i>Corpanthe pachyrrhiza</i> K. Schum. (3075) and other species of <i>Pachystylia</i>)	—	—	—	—	—	—	—	—
Idagbon, Abo	<i>Conopharyngia penduliflora</i> Stapf (9, 3076, 3332)	5	—	—	—	—	—	—	5
Idagbon, Abo	<i>Terminalia ivorensis</i> A. Chev.	—	2	—	—	—	—	—	1
Idagbon, Abo	<i>Entandrophragma macrophyllum</i> A. Chev.	1	—	—	—	—	—	—	1
Idagbon, Abo	<i>Chlorophora excelsa</i> (Welw.) Bth. & Hook. f.	—	1	1	—	—	—	—	1
Idagbon, Abo	<i>Allanblackia</i> or <i>Pentadesma</i> sp.	—	—	—	—	—	—	—	—
Idagbon, Abo	—	1	—	—	—	—	—	—	1
Idagbon, Abo	—	5	5	5	2	1	—	—	18
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—	—	—	—
Idagbon, Abo	—	—	—	—	—	—			

Itako Pupa	<i>S. reticenia</i> S. Moore (3294*) (and <i>S. grandifolia</i> Hook. f. (174)?)	66	92	17	1	—	—	176	1
Jesebe or Akika	<i>Discoglyprena caloneura</i> (Pax) Prain (3221, 3340)	11	6	1	—	—	—	18	—
Agba	—	4	1	2	—	—	—	7	—
Kalado	<i>Homalium</i> sp.	1	1	1	—	—	—	2	—
Lapawe	—	8	—	1	2	—	—	12	3
Odoko	<i>Scottellia kamerunensis</i> Gilg (15, 78, 125, 194, 234, 3271, 3431, 3452) and/or n.sp. (161, 3432) and other species of <i>Scottellia</i> ?	2	—	—	—	—	—	2	—
Ofuye	Guarea Thompsoni Sprague & Hutch.	—	—	1	1	—	—	3	2
Ogunwo	<i>Akaya torrensis</i> A. Chev. (141, 147)	—	2	—	—	—	—	2	—
Ogun	<i>Uvariastrom</i> sp. cf. <i>Pirreanum</i> Engl. (3264)	1	1	—	—	—	—	2	—
Ogwagwa or Keso	<i>Diospyros chrysanthia</i> Gürke (72, 3213, 3331)	2	—	—	—	—	—	2	—
Ojojo Onode	<i>Mariya micrantha</i> Muell. Arg. (157, 3193)	3	—	—	—	—	—	3	—
Kotale	<i>Barteria fistulosa</i> Mast. (127, 171) (and/or <i>B. nigriflora</i> Hook. f.)	1	2	—	3	—	—	6	3
Okoro	<i>Drypetes Amoracia</i> Pax & K. Hoffm.	2	1	2	1	—	—	8	4
Okuba	—	1	—	—	—	—	—	2	—
Okepo	? <i>Garcinia ovalifolia</i> Oliv. (154)	19	2	—	—	—	—	21	—
Olofin	<i>Guarea cedrata</i> (A. Chev.) Pellegr.	6	3	1	—	1	—	11	1
Olorin	<i>Sterculia Traquecantha</i> Lindl.	1	—	—	—	—	—	1	—
Omorin	<i>Xylopia Quinitas</i> Engl. & Diels (88, 3159, 3334, 3434)	1	—	2	—	—	—	3	—
Opele	<i>Sarcocaulis Diderichii</i> De Wild. (3276)	1	—	—	—	—	—	1	—
Oporoporo Dudu	? <i>Cola cordifolia</i> (Cav.) R. Br.	2	—	—	—	—	—	3	1
Oro or Oriso	<i>Antiaris africana</i> Engl.	—	—	—	1	—	—	1	1
Oropa or Erubabaseje	<i>Staudtia stipitata</i> Warb.	1	—	2	—	—	—	3	—
Osho Pupa	<i>Enantia chlorantha</i> Oliv.	3	—	1	2	—	—	6	2
Oshun	<i>Diospyros insculpta</i> Hutch. & Dalz. (90, 155, 186, 3480, 3486)	46	16	—	—	—	—	63	—
Owewe	Combretodendron africanum (Welw.) Exell	1	2	1	1	—	1	6	2
Sida	Lorova Klaineana Pierre ex Sprague	2	—	—	1	—	—	3	1
(Unknown I)	—	1	—	—	—	—	—	1	—
(Unknown II)	—	265	178	69	36	9	25	582	70

II Shrubs and herbs

(a) Shrubs

<i>Clerodendrum Whitfieldii</i> Seem. (103)	f.	<i>Psychotria</i> sp. (3307*, prob. = 3385 on S.P. 2)	l.f.
? <i>Icacina trichantha</i> Oliv. (3142, etc.)	o.	Rubiaceae I (or tree seedling?)	r.
<i>Memecylon membranifolium</i> Hook. f. (3179, 3305*)	f.	Rubiaceae II	r.
<i>Rinorea</i> sp. (3303*, prob. = 3171 on S.P. 1 and 3252 on S.P. 4)	a.	<i>Thominnia sanguinea</i> Vahl (3011, 3421)	r.
<i>Rinorea</i> sp. (prob. = 3172 on S.P. 1 and 3252 on S.P. 4)	r.	<i>Trichostachys</i> sp. (3313*)	o.
<i>Rinorea</i> sp. (3315*)	r.	(ii) Monocotyledons:	
<i>Sphenocentrum</i> sp. cf. <i>Jollyanum</i> Pierre (3304*)	r.?	Araceae	r.
<i>Drypetes melanodiana</i> Pax & K. Hoffm. (3320, 3139) (Unidentifiable, 3310)	o.	<i>Corymborrhiz Wleiischii</i> (Reichb. f.) Ktze. (3312*)	r.
	v.a.	<i>Palisota ambigua</i> (Beauv.) C. B. Clarke (3141)	l.f.
		<i>P. Barteri</i> Hook. f. (53, 3184, 3339)	f.-a.
		<i>Polyspatha paniculata</i> Bth. (3176)	l.f.
		Zingiberaceae?	l.a.

(b) Herbs (excluding epiphytes)

(i) Dicotyledons:	l.a.	(iii) Ferns:	r.
<i>Geophila hirsuta</i> Bth. (3167, 3186, 3304*, 3384, 3402)	l.f.	<i>Bobbitis auriculata</i> (Sw.) Alston (3242, 3316*, 3393)	o.
<i>Geophila</i> sp. (3311*)	l.f.	<i>Dryopteris protensa</i> (Alz.) C. Chr. (3169, 3306*)	
<i>Grumitia</i> sp. (3314*)	l.f.		
<i>Grumitia</i> sp. (3318*)	l.f.		
<i>Laportea</i> sp. (3316*)	l.a.		
<i>Psychotria neurodictyon</i> K. Schum. (3300)			

Table IX. Sample Plot 4. Fresh-water Swamp Forest
About 8 km. north of Akilla, Shasha Forest Reserve (Ijebu Province)

Vernacular name	Species	Diameter class						Total no. of individuals 4 in. (10 cm.) diameter and over	Total no. of individuals 16 in. (41 cm.) diameter and over
		4-7 in. (10-19 cm.)	8-11 in. (20-29 cm.)	12-15 in. (30-40 cm.)	16-19 in. (41-50 cm.)	20-23 in. (51-60 cm.)	24 in. and over (61 cm. and over)		
Abura	<i>Mitragyna stipulosa</i> Ktze. *	17	14	15	5	12	9	72	26
Afara	<i>Terminalia superba</i> Engl. & Diels (3040)	1	—	—	—	—	—	1	—
Agba Irooun	<i>Raphia pubescens</i> Hook. f. (3006)	1	—	—	—	—	—	1	—
Agbawu	<i>Musanga Smithii</i> R.Br.	2	—	—	—	—	—	4	—
Ahun	<i>Alstonia congensis</i> Engl.	3	3	4	3	2	4	19	9
Ajeleru	<i>Cassipouira glaberrima</i> (K. Schum.) Hiern (139, 187)	2	—	—	—	—	—	2	—
Akila	<i>Isoloma</i> n.sp. ? aff. <i>campanulata</i> Engl. & Diels (3343)	1	—	—	—	—	—	1	—
Apado (swamp kind)	<i>Berlinia Heudelotina</i> Baill. var. <i>congolensis</i> Bak. f. (179)	3	—	3	—	—	—	6	—
Atole	<i>Sapium ellipticum</i> (Hochst.) Pax (250)	—	—	2	—	—	—	2	—
Awasa Aragba	<i>Bridelia micrantha</i> Baill. (3282)	—	3	4	6	—	—	13	6
Awasa Odida	<i>Macaranga Barteni</i> Muell. Arg. (3246)	1	1	—	—	—	—	2	—
Ebo	<i>Casuarina brachyoides</i> Mildbr. ex Hutch. & Dalz. (69, 3046, 3302, 3370, 3374)	21	7	2	4	—	—	34	4
Egogo	<i>Carapa procera</i> DC. (3013)	1	—	—	—	—	—	1	—
Ekti	<i>Lophira procera</i> A. Chev.	—	—	—	—	—	5	5	—
Epimpa Iroko	<i>Ricorea</i> sp. cf. <i>dentata</i> (Beaur.) Ktze. (58, 113, 3426) (and other sp.?)	1	—	—	—	—	—	1	—
Epowu	<i>Neoboultonia glabrescens</i> Prain (3203*)	13	12	1	—	—	—	26	—
Erikesi	<i>Diospyros monbutsensis</i> Gürke (18, 3204* 3329)	1	—	—	—	—	—	1	—
Erin	<i>Pteroloma umbellata</i> (Stapf) Stapf (8, 142, 3162, 3211)	6	—	—	—	—	—	6	—
Esununapon	<i>Diospyros confertiflora</i> Gürke (191, 3443)	5	1	—	—	—	—	6	—
Gbinbindo	<i>Pterocarpus santalinoides</i> L'Her. (3218, 3322)	1	—	—	—	—	—	1	—
Idagbon, Ako	<i>Corynanthe pachyceras</i> K. Schum. (3075) (or <i>Pausingstalia</i> sp.)	—	—	1	—	—	—	1	—
Jesabe or Akika	<i>Disoclyprema caloneura</i> (Pax) Prain (3221, 3340)	3	—	—	—	—	—	3	—
Agba	<i>Homalium</i> sp. ? <i>africanum</i> Bth. (3279)	17	2	1	—	—	—	20	—
Kalado	—	5	3	—	—	—	—	8	—
Laposara	<i>Spondianthus</i> sp. cf. <i>S. ugandensis</i> Hutch.	88	39	8	10	2	—	147	12

* See note, p. 45.

A *RIVULARIA BULLATA*-*BALANUS* COMMUNITY

By T. KENNETH REES, *University College of Swansea*

DURING August 1937, whilst investigating the distribution of marine algae in the neighbourhood of the Lizard (Cornwall), a remarkable and quite isolated patch of *Rivularia bullata* Berk. was encountered inhabiting rocks occurring on Kennack Sands. No trace of this alga was to be found along the whole length of approachable coastline from Treleaver Cliff to Kynance Cove, yet at Kennack it grew so abundantly as to be the dominant plant on the rocks which outcrop from the general level of the sand. These rocks occur in the lower littoral region at the western end of the beach, lying inshore from Crig-a-Tana Rocks (Ordnance Survey 6 in., Cornwall, Sheet LXXXV N.W. and S.W.). They are but poorly colonized by marine algae, and at the particular level at which *Rivularia* grows, such algae as occur exist in scattered patches only.

Practically without exception *Rivularia* was found growing on *Balanus balanoides*. At times the growth of individual plants, or of gregarious tufts, was sufficiently extensive as to obscure the underlying rock completely, but upon examination it was found that their region of attachment was always fixed to the shells of *Balanus*.

The *Rivularia* community reached its upper limits at the base of the zone of *Fucus spiralis* L. amongst whose weather-beaten stipes a few scattered colonies were to be found growing on *Balanus*. On rocks devoid of *Fucus spiralis*, the upper limit strayed into the zone of *Lichina pygmaea* (with associated *Enteromorpha minima* Naeg.). Since *Balanus* itself spreads upwards well into the zone of *Pelvetia*, these observations seem to indicate that the greatest amount of exposure (i.e. emergence) which *Rivularia bullata* can withstand coincides with the upper part of the *Fucus vesiculosus* belt, which on less exposed rocks, follows upon that of *F. spiralis*. Using the terminology of Coleman (1933), the upper limit can be placed just a little below mean high-water neap tide (M.H.W.N.).

The community extends downwards to the edge of the zone of *Gigartina stellata* Batt. but does not penetrate below this level. The band of *Laurencia pinnatifida* Lam., which along this part of the coast occurs next above that of *Gigartina*, is frequently penetrated by *Rivularia*, so that the lower limit of the community may be placed between mean low-water springs and extreme low-water springs (see Coleman, 1933).

Within these limits, the community flourishes on rocks which, save for occasional *Laurencia* and *Lichina* plants, and occasional patches of *Verrucaria mucosa*, are devoid of algal vegetation. The Mollusca *Patella vulgaris* and *Mytilus edulis* occur here and there, the former frequently bearing *Enteromorpha compressa* Grev. The rocks for the most part rise up sharply from the

level of the sandy shore, and reach varying heights, but they are all covered at high water of ordinary tides. The more low-lying rocks are in places colonized by the sand-binding *Rhodochorton floridulum* Naeg., and since this prevents the settling of *Balanus* spat, no *Rivularia* is to be found in such areas.

The association of *Rivularia bullata* with *Balanus balanoides* is apparently unusual. Cotton (1912, p. 27) states: "During the summer (July–Sept.) a fine growth of *Rivularia bullata* is frequently found epiphytically upon *Lichina pygmaea*. In 1911 it was unusually abundant, being noted in August on all exposed parts of the mainland and Clare Island. *R. bullata* is not confined to the *Lichina* patches, but occurs on bare rocks. It sets in about half-tide level and continues to low water mark." References to any conspicuous growth of *Rivularia bullata* do not occur in recent literature relating to the ecology of marine algae, though its occurrence is mentioned in several local lists. During work conducted at Lough Ine (Rees, 1935) occasional individuals were found near the mouth of Barloge Creek (a fairly exposed type of coast), but in no case in sufficient quantity to form a local society.

The occurrence of this *Rivularia-Balanus* community at Kennack gives rise to a number of ecological considerations, more particularly as featuring an instance of biotic reactions and as emphasizing the importance of considering the sea shore as a biotic community or biome. Like many other marine Myxophyceae, *Rivularia bullata* is sporadic in its appearance, and a matter of considerable interest is its mode of inter-seasonal or inter-annual existence—the more so in this case as it appears to be so completely dependent upon *Balanus*. The recent work of Moore (1933, 1934) has shown that the shells of *Balanus* may be colonized by algae when they are from 4 to 6 months old. Spat usually settle during March and April and algal infection may begin in September. Moore and Parke (1934) found mainly prostrate or penetrating species, but do not record any large epizootic species finding lodgement on the surface of the shell. The genus *Rivularia* propagates both by hormogones and spores, the former undoubtedly provide an effective method for increasing the size of the colony and for the formation of new colonies during the favourable season, the latter for tiding over the inter-seasonal period. It would appear that up to the present there has been no record of spores being produced in *Rivularia bullata*, but amongst the material collected in Cornwall there were frequent instances of spores occurring either singly or occasionally in pairs, next to the basal heterocyst. Unlike the spores of fresh-water species, the walls of these spores were but very slightly thicker than those of the cells lying behind, and it appears to be probable that no thick-walled resting spore is formed. Some of the material collected was kept in a bottle containing sea-water during September. The sides of the bottle facing a window were found, after 10 days, to bear small bluish green patches. Upon examination they were found to consist of a mixture, in varying proportions, of three blue-green algae: *Phormidium* sp., *Lyngbya* sp. and sporelings of *Rivularia*. The presence of *Phormidium* and of *Lyngbya* was due probably to their living in the

gelatinous sheaths of the *Rivularia* colonies—a feature which is quite common amongst the more gelatinous Myxophyceae.

Like practically all marine algae, therefore, the spores (and also the hormogones) of *R. bullata* do not undergo a period of rest, but appear to germinate almost immediately after release. From the condition of the colonies in the bottle, it would appear that the release of the spores and hormogones is due to their partial decay, the fairly tough and firm outer region of the colony having become gelatinized and much softer. By the end of October, most of the colonies had disintegrated, but after the first fortnight there was little or no new growth on the sides of the bottle.

Under natural conditions the minute germlings, whether from spores or hormogones, would find easy lodgement on the roughened surfaces of *Balanus*. From analogy with the now quite well-known adelophycean stages recorded in the life history of many Phaeophyceae, the germlings would remain in a quiescent condition until the favourable season returned, when by repeated hormogone formation the typical adult colony would reappear. From an examination of slides kept in repeatedly renewed sea water, the favourable season for further development appears to be early in May, for at this time of the year minute round solid colonies of *Rivularia* became conspicuous on some of the slides on to whose surfaces had been scraped some of the bluish-green encrustation that appeared on the sides of the bottle in September.

An examination of the *Balanus* shells *in situ* showed that they were of varying ages, apparently in their second or third year of growth. The young white-shelled individuals developed from the 1937 spat were not effected. This would appear to confirm the suggestion made above—that is that the spores or germlings were already present on the older shells, or alternatively that the surfaces of young barnacles in their first months of growth—when the growth rate is quite rapid and deposition of calcareous material is extensive (Moore, 1933–4)—are unsuitable for the lodgement and consequent germination of spores or hormogones which might arrive with any spring invasion. Such an invasion, colonizing the one- or two-year-old barnacles, would account for the origin of the community if no adelophycean stages were already present. As a general rule, however, the autumn is the period of greatest vegetative activity amongst the marine Myxophyceae (Rees, 1935), and it therefore seems more probable that minute plantlets, similar to those found on the sides of the bottle and subsequently transferred to the glass slides, are developed in autumn. These, finding ready and immediate lodgement on the shells of *Balanus*, tide over the period of eclipse of the adult colonies.

It is natural to expect that such plantlets would germinate equally well on the bare rock surface, or epiphytically upon neighbouring algae. As to the first, the very steep angle of slope of the rock and the constant tituration by sand particles from the beach out of which the rocks arise are two factors which would mitigate against the establishment of germlings. The second

possibility is somewhat remote owing to the very sparse development of algae already referred to. An exception, however, must be made in the case of *Lichina pygmaea* which is—in patches—quite abundant at the upper limit of the *Rivularia-Balanus* community. Cotton (1912) reports that *Rivularia* is abundant on *Lichina* and at Lough Ine such *Rivularia bullata* as occurs is usually epiphytic on this marine lichen. It is difficult to understand why the lichen surfaces have been avoided at Kennack. To some extent there is competition with the epiphytic *Enteromorpha minima*, but this is quite insufficient to account for the complete lack of *Rivularia* colonies on *Lichina*. It may well be therefore that this particular species of *Rivularia* is a biologic form with physiological properties (as for instance in many of the smuts, rusts and moulds amongst the fungi) which result in an antithetic relationship with *Lichina*, and possibly neighbouring algae also. The slight differences in measurements of the trichomes are barely sufficient to warrant the suggestion of a new variety. In colour of trichome, in shape, size and consistency of the colony, the Cornwall *Rivularia* corresponds closely to that gathered at Lough Ine, and to the description of the alga in standard texts.

Phillips (1931, 1935), Clements (1916), Shelford (1931), Kitching (1935, 1937) and other ecologists have in recent years laid increasing stress upon the necessity of treating the community as a biotic entity rather than as a plant or animal one with external biotic factors. In a paper shortly to be published dealing with the colonization by *Porphyra*, *Bangia*, *Enteromorpha* spp., *Balanus*, *Pomatoceros*, *Campanularia* and other genera, of newly constructed concrete piers and pillars, the intimate and integrated biotic reactions which determine the trend of colonization will be dealt with fully. This short account of a *Rivularia-Balanus* community provides evidence of the importance of a study of both adelophycean stages and biotic relationships in attempting to elucidate problems connected with marine ecology of the littoral region.

REFERENCES

- Clements, F. E. Plant Succession. *Publ. Carneg. Instn.*, no. 242, 1916.
 Coleman, J. "The nature of the intertidal zonation of plants and animals." *J. Mar. Biol. Ass.* N.S. 18, 435, 1933.
 Cotton, A. D. "Marine algae." Clare Island Survey, Part XV. *Proc. Roy. Irish Acad.* 31, 1, 1912.
 Kitching, J. A. "An introduction to the ecology of intertidal rock surfaces on the coast of Argyle." *Trans. Roy. Soc. Edinb.* 58, 351, 1935.
 Kitching, J. A. "Studies in sublittoral ecology. II." *This JOURNAL*, 25, 482, 1937.
 Moore, H. B. "The biology of *Balanus balanoides*. I. Growth rate in its relation to size, season and tide level." *J. Mar. Biol. Ass.* N.S. 19, 851, 1933-4.
 Moore, H. B. & Parke, M. W. "The biology of *Balanus balanoides*. II. Algal infection of the shell." *J. Mar. Biol. Ass.* N.S. 20, 49, 1934.
 Newton, L. *A Handbook of British Seaweeds*. Brit. Museum, London, 1931.
 Phillips, John. "The biotic community." *This JOURNAL*, 19, 1, 1931.
 Phillips, John. "Succession, development, the climax and the complex organism: an analysis of concepts. III." *This JOURNAL*, 23, 488, 1935.
 Rees, T. K. "Marine algae of Lough Ine." *This JOURNAL*, 23, 69, 1935.
 Shelford, V. E. "Some concepts of bioecology." *Ecology*, 12, 485, 1931.

PERCENTAGE FREQUENCY AND QUADRAT SIZE IN ANALYTICAL STUDIES OF WEED FLORA

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(With four Figures in the Text)

INTRODUCTION

THE use of quantitative methods in analytical studies of vegetation has led to various investigations on the relations between the percentage frequency and density of the species and between the quadrat size and average number of species. Consequently, various empirical determinations of the relations and mathematical formulations arising out of theoretical considerations have been made.

Since its introduction by Raunkiaer in 1909 the method of percentage frequency has been widely used in studies on plant communities. The older view of du Rietz and his co-workers (1920) has been criticized by Kylin (1926), Pearsall (1924), Romell (1920, 1923, 1926, 1930) and others who have shown on theoretical grounds that the relation between percentage frequency and density is not linear. The du Rietzian concept has again been criticized by Ashby (1935), who from field data has confirmed the approximate logarithmic relation between percentage frequency and density (Kylin, 1926). Clapham (1936) however points out the limitation that although the relation is logarithmic, the density of a given species cannot be calculated accurately since the species vary greatly in their mode of distribution.

In a study of the distribution of species on grassland associations, Blackman (1935) shows that when the distribution of individuals of a species is at random or nearly so, the logarithm of percentage absence is directly proportional to density. He, therefore, recommends the use of percentage absence in ecological studies of plant associations. Clapham (1936), on the other hand, believes that, even if there is such a relation, the slope of the line cannot be calculated *a priori*, but must be determined by direct observations and that for each species separately since it seems that the mode of the distribution of the individuals of many species changes with density.

With regard to the relationship between the size of the quadrat and the average number of species found within the quadrat, it has been found (cf. Arrhenius, 1920, 1921, 1923; Gleason, 1920, 1922, 1925; Woollet *et al.* 1925; Hanson & Ball, 1928, etc.) that as the area of the quadrat is increased the number of the species also increases rapidly, but a corresponding increase in

the number of species is not maintained when the area of the sampling quadrat becomes relatively large.

Empirical determination of the nature of the relation has been made by Arrhenius (1920, 1921), Gleason (1922, 1925) and Palmgren (1916), but their conclusions have been the subject of criticism by Blackman (1935) on the basis that their grouping of the data of a large number of quadrats of a single size either at random (Arrhenius) or grouping at random of contiguous quadrats though not adjacent (Gleason) disagree with either the observed or calculated data.

Some investigators (Romell, 1920; Kylin, 1926; Wicksell, 1924; etc.), on the other hand, have endeavoured to deduce the relation from theoretical considerations assuming that the individuals of all the species are distributed at random. Blackman (1935) however observes that the agreement between the field and calculated data is not good, but is considerably improved if the less common species are omitted. Clapham (1936) also finds this disagreement and correlates it with the prevalent aggregation amongst the individuals of the species as determined by him in grassland communities of prairie vegetation.

In a statistical study of the weed flora on arable land (Singh & Das, 1938) opportunity was availed to study these problems as they relate to the distribution of weed species on arable land left fallow for some time—the subject of the present paper—since advantage could be taken of the knowledge of the mode of distribution of the individuals of the various weed species.

PERCENTAGE FREQUENCY AND DENSITY

The technique in the collection of data for investigating this relationship consisted in counting the number of individuals of the different weed species in a 6 × 6 in. quadrat thrown at random. 100 samples were taken from each of the five similar plots that were left fallow for some time from the end of a *Rabi*¹ season to the beginning of the same season next year.

On the assumption of the random distribution of individuals of species, the probability of not finding an individual (q) is

$$q = e^{-m},$$

where m is the mean density; and the probability of finding one or more individuals in a quadrat (p) is

$$p = 1 - q = 1 - e^{-m}.$$

Thus, the percentage frequency is related to density by the equation

$$m = -\frac{\log_e q}{k},$$

i.e. the relation between percentage frequency and density is logarithmic.

¹ *Rabi* season means the winter crop season which begins early in October and lasts up to the end of March.

In Fig. 1, where $\log_e q$ is plotted against the corresponding density (individuals per quadrat) of each species, it is seen that the points lie more or less scattered round the line drawn from theoretical considerations. Thus this proximity of the observed points to the calculated line establishes the approximate logarithmic relationship between the percentage frequency and density as obtained from theoretical considerations. But it is to be mentioned that in

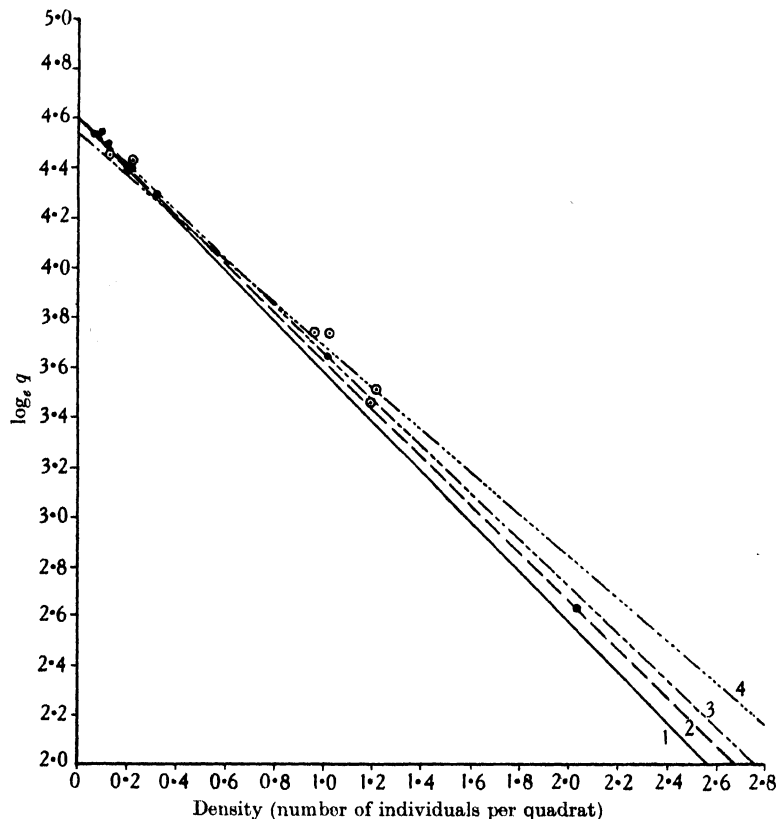


FIG. 1. Densities (individuals per quadrat) of the weed species plotted against their logarithm of percentage absences. Dots represent those species whose frequency occurrence fitted in significantly with the calculated Poisson series terms ("random species") while the circles with the centres represent the other set of species ("non-random species"). The continuous line (1) represents the line drawn from theoretical assumptions, while the other lines, 2, 3, 4, represent the fitted lines for all the species, "random" and "non-random" species respectively.

a previous study (Singh & Das, 1938), it has been found that although the comparison with the Poisson series terms by determining the goodness of fit of the observed and calculated data by the χ^2 test shows that the majority of the species are distributed at random, the determination of the relative variance indicates on the other hand that a slight degree of heterogeneity is detectable in all the species (Table III).

A further examination of the data (Fig. 1) reveals that the points representing the species *Bonnaya veronicaefolia*, *Euphorbia hirta*, etc., which are characterized by a probability of less than 0.5 for the χ^2 test for agreement with the Poisson series terms (Table III), lie farther apart from the theoretical line, whereas the points for species showing a significant fit with the terms of a Poisson series lie nearer to the theoretical line.

One can fit straight lines for the percentage absence against the observed densities of all the species and, also, of the species divided into two groups according to whether the fit of the calculated Poisson series terms with the observed field data is good (i.e. significant) or not. When this is done (Fig. 1), it is observed that the slopes of these lines differ both amongst themselves and

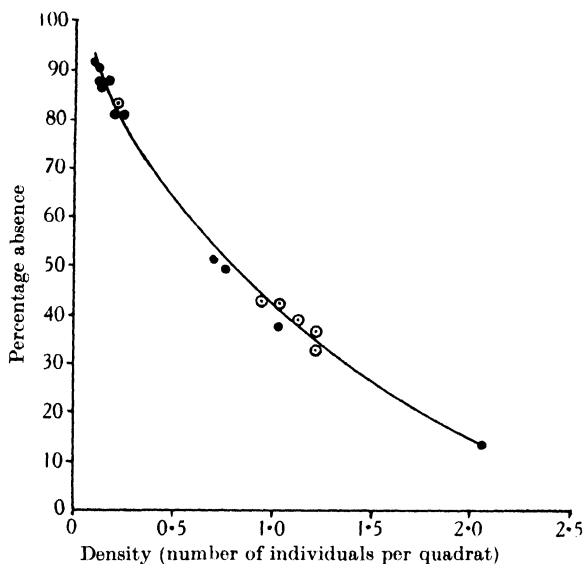


FIG. 2. Density (individuals per quadrat) of weed species plotted against their percentage absence. Dots represent the "random" species and circles the "non-random species".

also from the theoretical line. This difference in the slopes of the fitted lines from the theoretical line confirms the idea that the linear relation is only approximate. It has however to be borne in mind that the estimations of density and percentage frequency have errors attached to them. It is interesting to note further that with higher values of $\log_e q$ corresponding to lower values of density (individuals per quadrat) the fitted lines representing all the species and also the species for which the goodness of fit of the Poisson series terms is significant do not differ appreciably from the theoretical line, whereas for the fitted straight line representing the other set of species, the divergence appears to be greater (Fig. 1). In Fig. 2 the relation between percentage absence and density (individuals per quadrat) of all the species is graphically represented.

The species *Bonnaya brachiata* was selected because of the high mean density to test the above relation in the case of a particular species. The population was sampled with a quadrat of 50 cm. square divided into a lattice of 25 subsquares, each of 100 sq. cm. Observations were recorded on the total number of individuals in the quadrat and the number of empty squares. 100 such quadrats were selected at random in each of the five plots where the other data were recorded.

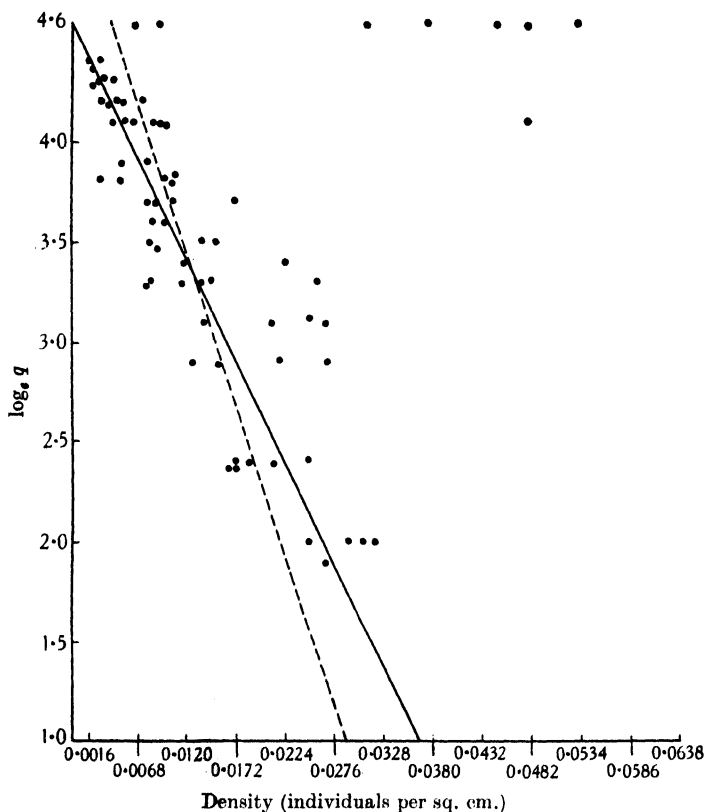


FIG. 3. Density of *Bonnaya brachiata* (individuals per sq. cm.) plotted against the logarithm of percentage absence. Continuous line represents the line drawn on theoretical assumption and the broken line represents the fitted line.

In Fig. 3 the values of density (individuals per sq. cm.) are plotted against $\log_e q$, where q is the chance of not finding any plant in a square. The theoretical line has been drawn on the assumption of the random distribution of the species from the relation

$$x = -\frac{\log_e q}{k},$$

where x = density, and k = size of the sampling area.

Since the points representing the observed densities (density per sq. cm.) lie scattered round the theoretical line (Fig. 3), it can be concluded that the relation between percentage frequency and density is approximately logarithmic. The slope of the fitted straight line differs from the theoretical line, which is to be expected since the determination of relative variance (Table III) indicates that a slight degree of heterogeneity is to be detected in the distribution of the individuals of this species.

DETERMINATION OF DENSITY OF INDIVIDUAL WEED SPECIES

It is known that provided the individuals of a species are distributed at random, the percentage absence of a species is given by the equation:

$$\text{Percentage absence} = e^{-m},$$

where m is the mean number of individuals per quadrat. But $e^{-m} = e^{-ky}$, where k is the density per unit area and y is the quadrat size. It follows therefore that if the percentage absence is known, the density of the species can be evaluated.

The density of each weed species is calculated (Table I) from the above relation since their percentage absences are known. The standard errors of both the observed and calculated densities and also the differences between the two values and their respective standard errors have been found (Table I) using the following formula as suggested by Bartlett (Blackman, 1935)

$$\sigma(\hat{k}) = \sqrt{(k/xy)},$$

where k is the density, x is the number of empty quadrats and y is the size of the sampling area.

Table I. *Observed and calculated densities of the various weed species*

Species	% absence	Density		Difference
		Observed	Calculated	
Bonnaya brachiata	14	2.04 \pm 0.143	1.96 \pm 0.140	0.08 \pm 0.028
Euphorbia erecta	52	0.69 \pm 0.083	0.653 \pm 0.081	0.037 \pm 0.019
Justicia diffusa	50	0.76 \pm 0.087	0.697 \pm 0.083	0.063 \pm 0.0251
Oldenlandia corymba	38	1.02 \pm 0.101	0.967 \pm 0.099	0.053 \pm 0.02
Corechorus acutangulus	73	0.32 \pm 0.057	0.314 \pm 0.056	0.008 \pm 0.0082
Indigofera enneaphylla	81	0.23 \pm 0.048	0.216 \pm 0.046	0.007 \pm 0.0138
Launea nudicaulis	82	0.20 \pm 0.048	0.198 \pm 0.044	0.002 \pm 0.0051
Trichodesma indicum	82	0.21 \pm 0.046	0.198 \pm 0.044	0.012 \pm 0.0012
Cleome viscosa	88	0.136 \pm 0.037	0.127 \pm 0.036	0.009 \pm 0.0096
Portulaca quadrifida	89	0.12 \pm 0.035	0.116 \pm 0.034	0.004 \pm 0.0064
Achyranthes aspera	90	0.116 \pm 0.034	0.105 \pm 0.032	0.0011 \pm 0.0106
Gynandropsis pentaphylla	92	0.086 \pm 0.029	0.083 \pm 0.029	0.003 \pm 0.0063
Boerhavia diffusa	93	0.08 \pm 0.028	0.073 \pm 0.027	0.0075 \pm 0.0081
Bonnaya veronicaefolia	33	1.21 \pm 0.11	1.108 \pm 0.105	0.102 \pm 0.032
Euphorbia hirta	32	1.20 \pm 0.109	1.13 \pm 0.106	0.07 \pm 0.024
Ammania brachiata	37	1.22 \pm 0.111	0.994 \pm 0.093	0.226 \pm 0.048
Desmodium triflorum	43	0.97 \pm 0.098	0.843 \pm 0.091	0.127 \pm 0.0363
Euphorbia thymifolia	42	1.02 \pm 0.101	0.867 \pm 0.093	0.153 \pm 0.0394
Phyllanthus Niruri	39	1.12 \pm 0.105	0.918 \pm 0.096	0.202 \pm 0.042
Alternanthera sissilis	83	0.216 \pm 0.046	0.186 \pm 0.043	0.030 \pm 0.0171
Vernonia cineria	85	0.18 \pm 0.042	0.162 \pm 0.040	0.018 \pm 0.0134

Examination of the data in Table I reveals that in general for those species where the p for the χ^2 test is greater than 0.05, the differences of the observed and calculated densities are not significant, while for those species where the odds against Poisson distribution are heavy the differences are significant. Of the latter category two exceptions appear. In *Alternanthera sissilis* and *Vernonia cineria* the standard errors of the differences of the observed and calculated densities are less than three times the actual difference, which indicates that the two values are not significantly different. The general conclusion that may be warranted from these estimations except for the two exceptions is that, for those species where the goodness of fit for the Poisson series terms is significant, the density may be estimated from the percentage absence of the species.

QUADRAT SIZE AND AVERAGE NUMBER OF SPECIES

Wicksell (1924), Kylin (1926), Blackman (1935), etc., have shown that on the assumption of the random distribution of all the species, the relationship between the quadrat size and the average number of species can be evaluated provided the percentage frequencies for any size of quadrat are known. If there are n species, the average number of species (\bar{N}_1) found in a single quadrat will be

$$\bar{N}_1 = n - [(1 - p_1) + (1 - p_2) + \dots + (1 - p_n)].$$

When the quadrat area is doubled, the average number of species (\bar{N}_2) for n species that will be found in the quadrat ($2x$) is

$$\bar{N}_2 = n - [(1 - p_1)^2 + (1 - p_2)^2 + \dots + (1 - p_n)^2].$$

Similarly, if the quadrat size is again doubled, the average number of species found is

$$\bar{N}_4 = n - [(1 - p_1)^4 + (1 - p_2)^4 + \dots + (1 - p_n)^4].$$

Thus, the expected number of species as the area of the original sampling quadrat is doubled or redoubled may be calculated if the percentage frequencies of all the species in an association are known for a quadrat of a given size.

Using data for the percentage frequencies obtained from 500 quadrats of 100 sq. cm. in area, the average number of species per quadrat of different areas has been calculated (Table II). When the observed and calculated mean number of species for the different quadrat sizes are compared (Fig. 4, curves 1 and 1₁), a marked disagreement between the two sets is noticed. This agrees with expectation since relative variances (Table III) indicate that the species are characterized by a slight degree of heterogeneity. It is seen that with the increase in quadrat size the calculated data show a higher average number of weed species than the field data. But when the less common species (species with frequencies of less than 20%) are omitted, the agreement improves considerably (Fig. 4, curves 2 and 2₁) so that both the calculated and observed mean number of species become almost the same although the tendency of a higher average value in the calculated series is consistently maintained throughout.

Table II. *Calculated and observed percentage frequencies in different quadrat sizes*

Species	100 sq. cm.	200 sq. cm.		400 sq. cm.		800 sq. cm.	
		Obs.	Cal.	Obs.	Cal.	Obs.	Cal.
Bonnaya brachiata	86	97	98	100	100	100	100
Euphorbia erecta	48	76	73	89	93	100	100
Justicia diffusa	50	81	76	95	94	100	100
Oldenlandia corymba	62	78	86	99	98	100	100
Corchorus acutangulus	27	38	45	51	70	62	91
Indigofera enneaphylla	19	32	35	48	58	57	82
Launea nudicaulis	18	29	33	46	55	56	80
Trichodesma indicum	18	23	33	44	55	59	80
Cleome viscosa	12	18	23	32	40	44	64
Portulaca quadrifida	11	16	21	29	38	39	62
Achyranthes aspera	10	15	19	24	34	41	56
Gynandropsis pentaphylla	8	11	15	19	28	31	48
Boerhavia diffusa	7	12	14	15	26	29	45
Bonnaya veronicaefolia	67	84	89	100	99	100	100
Euphorbia hirta	68	86	90	100	99	100	100
Ammania brachiata	63	81	86	98	98	100	100
Desmodium triflorum	57	79	82	99	97	100	100
Euphorbia thymifolia	58	78	82	95	97	100	100
Phyllanthus Niruri	61	80	85	91	98	100	100
Alternanthera sissilis	17	25	31	42	52	54	77
Vernonia cineria	15	22	28	36	48	49	73

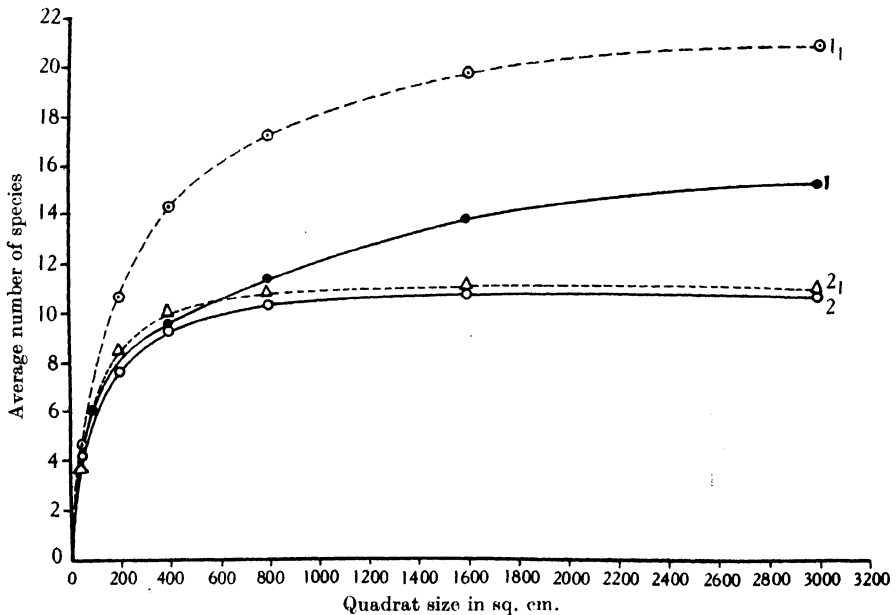


FIG. 4. The relationship between the quadrat size and the average number of species found in the quadrat based on field observations and calculations assuming a random distribution of all the species, 1 and 1_1 represent the observed and calculated data respectively when all the species are considered, while 2 and 2_1 represent the observed and calculated data when the less common species (species with a frequency of less than 20 %) are excluded.

Table III. *Probability for χ^2 test for Poisson distribution and relative variance of the different weed species*

Species	Probability for χ^2 test for Poisson distribution	Relative variance
Bonnaya brachiata	0.80	1.04
Euphorbia erecta	0.90	1.13
Justicia diffusa	0.70	1.18
Oldenlandia corymba	0.80	1.01
Corchorus acutangulus	0.70	0.93
Indigofera enneaphylla	0.50	1.5
Launea nudicaulis	0.80	1.0
Trichodesma indicum	0.70	1.04
Cleome viscosa	0.50	1.2
Portulaca quadrifida	0.80	1.1
Achyranthes aspera	0.50	1.1
Gynandropsis pentaphylla	0.80	1.1
Boerhavia diffusa	0.50	1.1
Bonnaya veronicaefolia	0.40	0.990
Euphorbia hirta	0.20	0.983
Ammania brachiata	0.10	1.3
Desmodium triflorum	0.05	0.907
Euphorbia thymifolia	0.20	1.15
Phyllanthus Niruri	0.04	1.21
Alternanthera sissilis	0.20	1.18
Vernonia cineria	0.30	1.2

It has been shown that if the percentage frequency (p) of a species showing random distribution is known for any size of quadrat (x), then the percentage frequency (p_1) of the same species in square quadrats of area y is given by the equation

$$p_1 = 1 - (1 - p) x/y.$$

Thus, the expected percentage frequencies of the various weed species for the different sizes of quadrats are calculated on the basis of the data obtained from 500 quadrats of 100 sq. cm. in area and are shown in Table II along with the observed percentage frequencies. Inspection of the data reveals that with the increase in the size of the quadrat, the percentage frequencies also increase. The calculated series, in general, shows an excess over the observed data. With the less common species (species with frequencies of less than 20%) also this disagreement becomes more marked when the larger quadrat areas (1600 and 3200 sq. cm.) are considered.

Blackman (1935) from a similar study confirms his conclusion that the less common species are not distributed at random. The present observations do not satisfy such a conclusion since most of the species, whether with higher or lower percentage frequencies, show a slight degree of heterogeneity in the distribution of the individuals as revealed by the determination of their relative variances (Table III). The rate of increase in the difference between the calculated and observed data is therefore a function of the abundance of the species and is not correlated with the exact mode of distribution of the species.

DISCUSSION

The present investigation has shown that the theoretical logarithmic relation between density and percentage frequency is found to exist also in the case of the weed species on arable land, the individuals of which could be counted at ease. The relation is, however, only approximately true since all the points are seen to lie scattered round the theoretical line. Such an approximate relation is to be expected, since in a previous contribution (Singh & Das, 1938) it has been shown that the weed species are not exactly distributed at random but are characterized by a slight degree of heterogeneity in the distribution of the individuals, as indicated by the determination of their relative variances.

The slope of the fitted straight line for all the species and also for each of the other two groups of species (random and non-random as judged by the goodness of fit test with the calculated Poisson series terms) differ considerably from the theoretical line. This is also observed to be true when the densities are plotted against the logarithm of percentage absence even in an individual species, viz. *Bonnaya brachiata*. This supports the contention made by Clapham (1936) that the slope of the line cannot be calculated *a priori*, but must be found by direct observation and that too for each species separately.

It is indeed interesting to observe that although strictly speaking all the species show a departure from the random distribution, those species that do not significantly fit in with the calculated Poisson series terms show a greater deviation from the theoretical expectation than the other group of species. This is demonstrated both by the fitted straight line for these species and also the determination of the significance of the expected density by the standard errors as calculated by the methods suggested by Bartlett (Blackman, 1935). This raises the important question as to how far the determination of the expected densities are to be regarded as valid in view of the prevailing heterogeneity in the distribution of the individuals of the species.

When the observed and calculated average number of species per quadrat of the different sizes are compared, it is observed that the disagreement between the two sets is lessened when the species with less than 20% frequency are omitted. Blackman (1935) considered such infrequent species to be distributed asymmetrically and explained the problem on this basis. But in the present investigation all the species are distributed more or less asymmetrically and hence Blackman's suggestion cannot be a complete explanation. In this connexion it has to be pointed out that Ashby (1935) has demonstrated that the division of species into percentage frequency classes gives a distorted measure of the abundance of the species in the vegetation. The mean area and the width of frequency class in mean areas increase as the percentage frequency decreases rapidly. Thus it may be held that the original quadrat size is largely responsible for the features under discussion.

The excess of the calculated percentage frequencies over the field data of the various weed species for the different sizes of quadrats also confirms the prevailing heterogeneity in the distribution of the species.

Besides the study of the structure of a static community, the aim of statistical ecology is to have a more precise knowledge in quantitative terms about floristic, density, luxuriance, etc., of vegetation as influenced by the different factors of environment. For such dynamic changes of vegetation with the influencing factors, correlating percentage frequency can not be used with any accuracy. Percentage absence has also to be used with caution more specially because of the variability of the density with the quadrat size. The determination of the correct size of the sampling area must be a prerequisite for such studies.

SUMMARY AND CONCLUSION

While investigating the distribution of the individuals of weed species in small plots of arable land which were left fallow for a short duration, the relationships between the percentage frequency and density and between the quadrat size and mean number of species have been studied.

The theoretical logarithmic relation between percentage frequency and density is found to exist also in the case of the weed species. But such a relationship is only approximately true since most of the weed species show a small degree of heterogeneity in the distribution of their individuals. This approximate relationship is also observed when the density and percentage frequency of an individual weed species, viz. *Bonnaya brachiata*, is studied.

When calculated and observed densities are compared by their standard errors as determined by the formula suggested by Bartlett, it is revealed that although the weed species are characterized by a slight degree of heterogeneity, the densities of some species may be determined. The difference between the observed and calculated densities is insignificant for those species where the agreement with the calculated Poisson series terms is significant. But for the other weed species where the χ^2 test indicates that the calculated Poisson series terms do not fit significantly, the calculated data differ significantly from the field data. Only two species, viz. *Alternanthera sessilis* and *Vernonia cineria*, are the exceptions to this latter category. These weed species however show a frequency of less than 20%.

When the relationship between the quadrat size and the average number of species found within the quadrat size is studied, a disagreement between the field and calculated data is revealed which however improves when the less common species are excluded. The disagreement is correlated with the heterogeneity in the distribution of the individuals of the weed species.

Due to the prevailing heterogeneity in the distribution of the weed species, the calculated percentage frequencies of weed species for varying quadrat sizes do not agree with the observed field data.

REFERENCES

- Arrhenius, O.** "Distribution of the species over the area." *Medd. K. VetenskAkad. Nobelinst.* 4, 56, 1920.
- Arrhenius, O.** "Species and area." *This JOURN.* 9, 95, 1921.
- Arrhenius, O.** "Statistical investigations in the constitution of plant associations." *Ecology*, 4, 68, 1923.
- Ashby, E.** "The quantitative analysis of vegetation." *Ann. Bot., Lond.*, 49, 779-802, 1935.
- Blackman, G. E.** "A study by statistical methods of the distribution of species in grassland associations." *Ann. Bot., Lond.*, 49, 749-78, 1935.
- Clapham, A. R.** "Over-dispersion in grassland communities and the use of statistical methods in plant ecology." *This JOURN.* 24, 232, 1936.
- Du Rietz, G. E., Fries, T. C. E., Osvald, H. & Tengwall, T. A.** "Zur methodologischen Grundlage der modernen Pflanzensoziologie Vetenskapl." *O. prakt. Vnders i Lappland*, 3, 1920.
- Fisher, R. A.** *Statistical Methods for Research Workers*. London: Oliver and Boyd, 1934.
- Gleason, H. A.** "Some applications of the Quadrat Method." *Bull. Torrey Bot. Cl.* 47, 21, 1920.
- Gleason, H. A.** "Relation between species and area." *Ecology*, 3, 158, 1922.
- Gleason, H. A.** "Species and Area." *Ecology*, 6, 66, 1925.
- Hanson C. & Ball, W. S.** "An application of Raunkiaer's Law of Frequency to Grazing Studies." *Ecology*, 9, 67, 1928.
- Kylin, H.** "Über Begriffsbildung und Statistik in der Pflanzensoziologie." *Bot. Not.* 2, 81, 1926.
- Palmgren, A.** "Studier over logangsomradena pa Aland." *Acta Soc. Fauna Flora fenn.* 42, 1, 1916.
- Pearsall, W. H.** "The statistical analysis of vegetation: a criticism of the concepts and methods of the Uppsala School." *This JOURN.* 12, 55, 1924.
- Raunkiaer, C.** *Life Forms of Plants and Statistical Plant Geography*. Oxford, 1934.
- Romell, L. G.** "Sur la règle de distribution florale." *Svensk bot. Tidskr.* 14, 1, 1920.
- Romell, L. G.** "Till Fragen om Frekvensfordelnings Regelns Tolkning." *Svensk. bot. Tidskr.* 17, 231, 1923.
- Romell, L. G.** "Bemerkungen zum Homogenitätsproblem." *Svensk. bot. Tidskr.* 20, 441, 1926.
- Romell, L. G.** "Comments on Raunkiaer's and similar methods of vegetation analysis and the 'Law of Frequency'." *Ecology*, 9, 20, 1930.
- Wicksell, A. S. D.** "Nagra formella synpunkter beträffande fordelingskurvorna inom vaxt-sociologien." *Bot. Not.* 1, 17, 1924.
- Woollet, E., Dean, D. & Coburn, H.** "Application of Gleason's formula to a *Carex lasiocarpa* association, an association of few species." *Bull. Torrey Bot. Cl.* 52, 23, 1925.
- Singh, B. N. & Chalam, G. V.** "A quantitative analysis of weed flora on arable land." *This JOURN.* 25, 213, 1937.
- Singh, B. N. & Das, K.** "Distribution of weed species on arable land." *This JOURN.* 26, 455, 1938.

TUSOCK FORMATION BY *SCHOENUS NIGRICANS*: THE ACTION OF FIRE AND WATER EROSION

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(With two Figures in the Text)

INTRODUCTION

THE autecology of the bog rush, *Schoenus nigricans* (Linn.), has been investigated in the neighbourhood of Oxford (Clapham & Dawkins, unpublished). This paper presents in summary form the substance of a certain aspect of that investigation, detached from the whole because the conclusions may prove of interest in the cases of plants other than *Schoenus*, in localities other than Oxford. It deals with Tussock formation, a widespread phenomenon on which published information appears to be scanty, although the methods by which tussocks are formed are probably numerous.

All arguments and conclusions are based on observations and experiments made chiefly in Cothill Marsh, Berks, between October 1936 and June 1937. Tussocks of *Schoenus* are very well developed and prominent in parts of this area.

GENERAL MORPHOLOGY OF *SCHOENUS*

Schoenus plants show much variation in size, but in the mature state always present the same appearance of stiff erect stems and leaves arising densely from circular clumps. Such "clumps" may be raised very conspicuously from the general soil surface, in which case they are (here) termed *tussocks*; or they may be on a level with the general surface, in which case they are termed *hummocks*. (These terms are used repeatedly throughout this paper, always in the same sense.)

The *Schoenus* plant consists of a more or less vertical branching stock bearing at the tips of the branches flowering stems, and laterally roots and leaves, with further branches subtended by some of the higher leaves. Aerial stems are always unbranched, normally up to a metre in height, and bear (each) a compact terminal head of black flowers. Leaves are similar in appearance to stems but are less tall, less thick, and always possessed of a brown or black sheathing base. The stock is slow growing, with short internodes of which up to four are produced each year. Branching is never regular, but can probably always be interpreted in terms of a sympodium.

The direction of branching is such as to make the direction of growth as nearly vertical as is compatible with the increasing growth in thickness. This extreme compactness, together with the toughness and persistence of the stock, is the most important cause of tussock formation by *Schoenus*.

TUSSOCK MORPHOLOGY

In a *Schoenetum* with large tussocks there are on the average slightly less than four tussocks per square metre; they are mostly cylindrical, but may narrow downwards, and reach a height of about 40 cm. from the ground between tussocks to the bases of the flowering stems and leaves at their tops. Diameters may reach 35 cm. at the top, and about 30 cm. at the bottom. In any tussocky *Schoenetum* the majority of tussocks appear equally large, but smaller ones occur among them.

A longitudinal section down the centre of a tussock shows a definite structure, providing a history of its development, and valuable evidence as to the nature of the habitat since its origin. This is on account of the persistence of the stock and leaf bases in an intact state from the earliest stages of the tussock.

Such a section shows that the stock occupies a cone at the centre of the tussock, tapering downwards. The shape of this cone accords directly with expectation from consideration of the method of branching of the stock, above referred to. We should in fact expect that increase in thickness would bear a logarithmic relation to increase in height according to some form of the compound interest equation. The actual numerical relationship has not been established, but the line of the outermost branches of the stock is definitely observed to spread outwards in the expected manner. This is illustrated in Fig. 1 which represents an actual specimen.

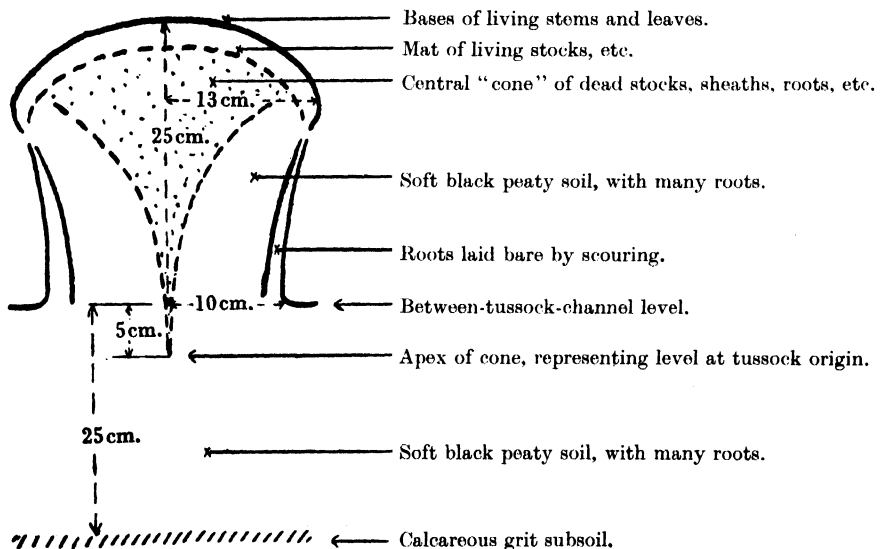


Fig. 1. Diagrammatic vertical section through centre of tussock of smaller dimensions than those given above.

The oldest part of the stock, as indicated by the apex of the inverted cone, is 5 cm. below the present level of the channel surrounding the tussock; from this beginning the stock grew upward and outward, the form meanwhile passing from a small caespitose hummock to a taller and thicker columnar tussock; the majority of roots growing downwards and tending to cause the columnar form. Scouring away of the soil around the outermost roots may on the other hand tend to cause "reversion" to the inverted cone form.

SUMMARY OF ECOLOGICAL STATUS OF TUSSOCKS

Schoeneta have been shown to occur around Oxford almost exclusively in depressions in the ground left after removal of fuel peat, in valley fens fed by calcareous streams. A peculiarity of these peat cutting habitats over other habitats locally is the possession of a water table constantly at or near the surface, with soil water saturated with calcium carbonate, or nearly so. It is concluded that the restriction of *Schoenus* to peat cuttings (as above referred to) is dependent upon these two main factors.

Establishment of *Schoenus* in the new peat cutting depends upon the water conditions prevailing, the seeds germinating only on a substratum at or closely above the water table. Thus stages leading to the dominance of *Schoenus* may be more or less numerous. After a stage of dominance of *Schoenus*, the latter becomes replaced by grasses, chiefly *Molinia caerulea*, whose centres of spreading are (in such habitats) always *Schoenus* clumps. In any *Schoenetum* which is subject to burning the dominance of *Molinia* is hastened.

Broadly, there are two types of vegetation at the stage of dominance of *Schoenus*:

(i) The "Caespitose" or "Hummocky" *Schoenetum*, in which the vegetation is continuous, containing *Schoenus* plants of all ages, but none raised appreciably above the general level, although the persistent stocks have been traced to about 20 cm. below the surface level.

(ii) The "Tussocky" *Schoenetum*, in which tussocks occur as above described, tall, columnar, closely spaced, quite individual, and with sparse vegetation between them.

It is a matter of general observation that around Oxford the first of the two types occurs where the floor of the cutting is level or nearly so, and the second where it is sloping. It must be clearly realized however that these terms, "hummocky" and "tussocky", are relative only, and although the two types may be separate from very early stages, they are essentially similar, and are liable to interchange. An attempt to explain their relationship forms the basis of the following section dealing with the mechanism of tussock formation.

ANALYSIS OF THE MECHANISM OF TUSSOCK FORMATION

Introductory

An account is here given of the supposed development of a certain *Schoenetum* in Cothill Marsh. Each step in the account is based either upon scientific principles, or upon steps which have gone before, or upon direct observation. In the latter case it would always be possible to refer to several independent pieces of evidence, but in most cases the quotation of one only is considered sufficient.

Tussock formation described

The *Schoenetum* to be considered covers a broad peat cutting along the edge of which flows a stream, about one-third of a metre in width, and slow-flowing. It consists for the most part of level hummocky *Schoenetum*, but a belt of tussocks forms a fringe 1 or 2 m. wide all along the edge of the stream. The tussocks immediately abutting on the stream are the tallest (above the soil surface), and the height decreases as the distance from the stream increases.

It is supposed that at one time the level of the stream running along the side of this cutting was considerably higher relative to the height of the vegetation than now; that the floor of the cuttings was level to the stream edge, and that *Schoenus* was thinly scattered through the vegetation, which was more or less uniform in height and more or less closed.

In time the height of the vegetation increased (by its own growth) and the level of water in the stream fell (by erosion of its bed). Proof of these processes is given by two observations: first, that the lowest *Schoenus* remains, though once at the surface, may now be down to 20 cm. below the soil surface; and, secondly, that rhizomes of *Juncus obtusiflorus*, once below the ground in the stream bed, are now left exposed, up to 5 cm. above the bed.

Water erosion. Water was continuously supplied to the cutting by seepage from the higher uncut ground "behind"; and the water table in the cutting was therefore kept at the surface, and varied little. Because most of the area was level, the water in the soil, and in small depressions at the surface, was stagnant or very nearly so; but in the neighbourhood of the stream the effect of the pair of processes above mentioned was a sharp slope in the ground, ever increasing in angle (and in breadth) as soil was laid down above and washed away by the stream below; as a result the water table in the slope was in a constant state of motion, and rain, instead of adding to the height of the table (as in level parts), only increased its rate of movement.

The result of this process was that the *Schoenus* plants growing along this belt were left as scattered and isolated clumps, growing upward from a sloping floor from which the looser peat soil formed by plants other than *Schoenus* was continuously being washed away; for *Schoenus*, being the only plant in the community with rigid, persistent, and vertically growing stocks, is the

only one to resist water erosion. This is amply proved by the 5 cm. difference between soil and anatomical base of tussocks referred to in a previous paragraph: this 5 cm. represents the depth of non-*Schoenus* peat laid down in a time sufficient for the accumulation of 20 cm. in level parts not subject to erosion (see (i) on p. 80). That water erosion is the active agent in causing this effect is proved by the discovery of *Juncus* rhizomes left exposed above the soil level between a certain pair of tussocks. These rhizomes were horizontal, and entered the tussocks at each end. No evidence can be found of rhizomes of *Juncus obtusiflorus* continuing horizontal growth in light.

Further increase in the general vegetational level, and further dropping of the stream level caused increased tussock height near the stream, and a widening of the belt covered by the gradient, with a corresponding increase in the number of *Schoenus* plants left sufficiently high to merit classification as tussocks.

The fire factor. When tussocks are once formed, they provide a habitat for adventives which require drier conditions than are to be found elsewhere in the marsh. The most important of these adventives is *Molinia*. A relevant character of this plant is its extreme inflammability; a great deal of foliage is produced in the growing season, and this becomes very dry during the summer immediately following. From one cause or another frequent fires occur. These have several effects upon the development of the habitat, which can easily be demonstrated. We may mention here:

(i) Tussock tops are the centres of burning, and the flora immediately around tussocks is diminished either by burning or by scorching. Therefore

(a) by slowing down the rate at which soil is laid down between tussocks, and (b) by exposing soil which is thereby more easily washed away by water, it contributes substantially towards the increase in height of tussocks above the ground; (c) the increased erosion rate (following from b) automatically extends the area subject to erosion, and extends the area likely to contain *Schoenus* in tussocks.

(ii) *Molinia* recovers quicker from burning than does *Schoenus*, therefore the dominance of *Molinia* on tussocks is accelerated.

(iii) The invasion of shrubs and trees is prevented.

These three effects, but especially the increase in height and number of tussocks, and increase in degree of dominance of *Molinia*, are all tendencies due also to other ecological factors than fire, which operate before the fire factor sets in, and which in fact create the susceptibility to burning in the first place. It is therefore obvious that once initiated (as a result of operation of these "primary" factors), the fire factor becomes more intense in a compound manner, each of the effects of burning increasing the susceptibility of the affected areas to burning in the future.

It is not likely that ecological factors other than these—growth phenomena and persistence of dead parts of *Schoenus*, and water erosion, accentuated

by burning—play any important part in the formation of tussocks; frost was ineffective in the winters 1936–7 and 1937–8, and although both of these were very mild winters, frost is unlikely to have important effect in differentiating the two habitat types. Rabbits however may contribute towards tussock development by having the same effect as (i) above; this might be due to the rabbits grazing elements of the vegetation between tussocks, unless (which is unlikely) this responds unchecked like lawn grass to a mowing machine; or it may be due to the inability of any or some members of this vegetation to withstand their trampling.

The following diagram summarizes the main points of this account. It shows vegetation levels in an imaginary line at right angles to the stream, passing through *Schoenus* plants, at various imaginary periods after the origin of the flora on the bare peat cutting floor, with corresponding levels in the stream bed. It must be remembered however that the diagram is highly idealized, and that proportions are entirely imaginary; it is intended as a simple illustration. It is not proposed that the intervals of time between the four levels be estimated.

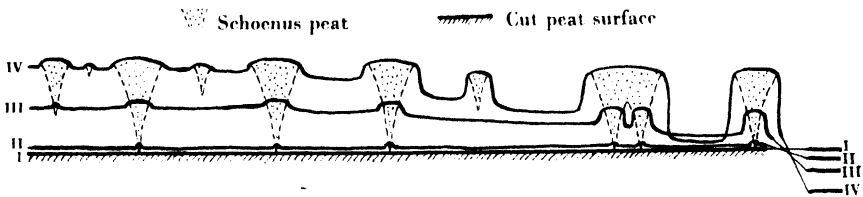


FIG. 2. Diagrammatic section of Schoenetum

Certain facts concerning the nature of tussock formation have been incorporated in the diagram without previous mention. The following especially require clarification:

(i) The rate of growth of *Schoenus* plants is not constant. It has been shown that the nearer the growing points are to the water, the greater is the rate of growth of the plant. Thus, although the tussocks abutting on the stream are the most conspicuous, their tops are less high above their origins than are the tops of the tussocks and hummocks of equal age in zones farther back, where water erosion has been less active, and where the height above the water table is consequently less great.

(ii) *Schoenus* plants both in hummocky and in tussocky parts of Schoenetum are of varying ages. It is fair to point out, however, that in a mature tussocky Schoenetum there is a remarkable uniformity of size of tussocks. This uniformity is due to the slowing off in the rate of growth as distance (of growing points) above the water table increases (as just referred to); for height plotted against age of tussocks would give logarithmic curves, steep at first, and then flattening, so that tussocks differing in age by many years would, if sufficiently old,

have the same order of height. Thus the apparent uniformity of height of the majority of tussocks is consistent with the hypothesis that some are much younger than others.

(iii) Although *Schoenus* seeds may germinate in any part of the habitat where water conditions are satisfactory, the chances of their development to maturity are limited. It has been said that vegetation on and in the neighbourhood of tussocks is the chief part of the flora to suffer damage by burning: but, whereas mature *Schoenus* plants survive the fiercest fires which occur (on account of the protection of their buds within the sheathing leaf bases), the seedlings on the other hand are extremely susceptible to burning. *Schoenus* plants have been known to survive to maturity in wet, hummocky Schoeneta where *Molinia* invasion is not advanced, and where fires do not spread; but in tussocky Schoeneta only in very wide spaces between tussocks, sufficiently far away from the tussocks which are the centres of burning. The existence of this factor is indicated in the diagram, but its effects are followed in greater detail in the second part of this paper.

TUSOCK DISPERSION: STATISTICAL ANALYSIS

The apparent uniformity of distribution of tussocks wherever tussocks occurred prompted a statistical analysis of tussock dispersion; for a significant demonstration of uniformity would indicate that the positions of tussocks were mutually dependent. Statistical data were obtained by examining a population of tussocks in the largest Schoenetum in Cothill Marsh.

A grid square with 10 m. sides was measured out in the Schoenetum, and divided into fifty small rectangles by means of string lines. The number of tussocks (to the nearest quarter tussock) in each of these 2-sq. m. rectangles was recorded in a chart of the square. This chart is reproduced below:

8	9	8	7	7
5	8	9	9	8
8	9	5	7	6½
5½	10½	10½	5½	8½ ½
7	8	8	12	6 ½
6	8	6	9	9
6	5	7	10	6
8	7½	6½	7½	8
10	8½	8½	7½ ¼	6½ ¼
13	8	8	8 ¼	8½ ¼

Statistical treatment

Analysis of variance. As summarized in the analysis of variance table below, the estimate of variance for row totals (mean square of rows), when compared with that for column totals by Fisher's z-test, shows that variation between rows is not significantly different from variation between columns; similarly, variation between either row totals or column totals is not significantly different from that between individual small squares after the effects

of variation between rows and columns have been eliminated (mean square residual represents this "residual variation").

Analysis of variance table

Variable	Degrees of freedom	Sum of squares	Mean square	z
Rows	9	22.12	2.4577	} Insignificant
Columns	4	4.57	1.1425	
Residual	36	111.78	3.1050	
Total	49	138.47	2.8259	

Therefore there are no trends in the population tending to concentrate tussocks in any direction in the square: in other words, in the area covered, the population of tussocks is homogeneous, and we are justified in using the data for direct tests as to the nature of tussock dispersion.

Tests for under-dispersion: (i) A test is supplied by a modification of the "Relative Variance" method used by Clapham (1936).

A frequency distribution of mutually independent events such as randomly dispersed vegetation units, follows a binomial frequency distribution; the chances of occurrence in samples 0, 1, 2, ..., n times being represented by the successive terms of the expanded expression; $(p + q)^n$, where

p = probability of occurrence (in the case of a unit of vegetation) on any one spot;

q = probability of failure of occurrence on any one spot.

It can be shown that in such a binomial:

The mean (m) = np .

Variance (V) = npq .

Therefore $V/m = q = 1 - p$.

Now the Poisson distribution is a special case of the binomial in which $p \rightarrow$ zero, and $n \rightarrow$ infinity. It therefore holds where the probability of an event (e.g. a unit of vegetation on any one spot) is infinitely small. In a perfect Poisson distribution, V/m is unity because p is zero.

It is legitimate to test for the existence of a Poisson distribution among units of vegetation if these units can be regarded as being of negligible area. Unlike the individual plants tested in this way by Clapham, however, the area of a tussock can in no way be considered negligible. Although tussocks originated from single seedlings, we cannot use this fact to justify application of the (simpler) Poisson test, because as has been stated (p. 83) tussocks are of varying ages; so that the freedom of distribution of these "tussock seedlings" has always been limited by the distribution of previously established tussocks, all of which had measurable areas.

In the case of such a tussock population the expression $1 - p$ represents the proportion of the total area expected to be bare of tussocks. For a random distribution of tussocks the estimate of V/m will tend to this value; and just as in the case of the Poisson distribution, estimates greater than this will

indicate over-dispersion, or greater patchiness, and estimates less will indicate under-dispersion, or greater evenness, than would be expected in a random population.

Calculated from the figures tabulated, for tussock distribution:

Mean (\bar{x}) = 7.84 (x = number in respective small squares).

Variance $\left(\frac{\sum (x - \bar{x})^2}{N - 1}\right) = 2.8259$ (N = number of small squares).

Therefore V/m = 0.3605.

The average area covered by individual tussocks has not been determined, but, taking the maximum figures given on p. 79 (maximum diameter = 35 cm.), the area covered by the top of a tussock can be calculated to be 0.0963 sq. m.; let us say 0.1 sq. m. as a maximum. Therefore an outside minimum estimate of the proportion of area bare of tussocks (taking the mean number of tussocks per sq. m. as 3.92) will be:

$$1 - p = 1 - (0.1 \times 3.92) = 0.608; \text{ let us say } 0.6.$$

This value of $q = 1 - p = 0.6$ has a standard error $\sqrt{pq/n}$ (where n is calculated from the assumption that the product np = the estimated mean). The standard error thus calculated approximately equals 0.11.

0.6 ± 0.11 would be the order of the V/m value were tussock dispersion to follow a binomial. The actual estimate of V/m being 0.36, and thus less than the expected value by more than twice its standard error, therefore indicates a high degree of under-dispersion, that is, a tendency towards uniformity in tussock distribution over the 100 sq. m. studied.

(ii) The actual distribution as recorded in the above chart, when compared with that of a binomial with the same mean by an approximate χ^2 test, was again found to show a very significant departure on the side of under-dispersion.

It is therefore a statistically valid conclusion that tussocks are more evenly spaced than is expected on the hypothesis of a random (binomial) distribution; their positions are mutually dependent, and/or dependent upon some other factor tending to control their distribution in the direction of uniformity.

DISCUSSION OF STATISTICAL CONCLUSION

It follows from paragraphs (ii) and (iii) on pp. 83-4 that present tussock distribution is the result of a period during which an equilibrium condition has been or is being reached; for at the beginning of the period tussocks were less densely scattered, and tussock primordia were therefore more widely spaced than present day tussock centres. It is impossible to know the type of dispersion of these original tussock primordia, but it can safely be assumed that they were not evenly scattered, but that they were random, or more

probably still, patchy or unevenly scattered.¹ These primordia will have developed into tussocks similarly dispersed.

All through the life of the community however there has been a closing in of the population of *Schoenus*; new tussocks have grown up, and the density (mean number of tussocks per unit area) has been increasing. But after a certain stage in development of the earliest tussocks, the "fire factor" began to play its part in limiting the survival and distribution of tussocks, as explained in (iii) (p. 84) we may repeat the observation that new tussocks grow up only in the larger spaces between existing tussocks, because seedlings in smaller spaces become scorched on account of the proximity of burning tussocks). It follows that while the density of the tussock population increased, there was a tendency for tussock distribution to become uniform, and after a certain stage to remain uniform with no increase in density, by the continued filling up of the larger spaces with more tussocks until all the spaces were so small that it was impossible for *Schoenus* seedlings to survive in any of them; until in fact the equilibrium referred to in the previous paragraph had been reached, and tussock density had reached a saturation value for the habitat.

It is of course impossible to suppose that the minimum distance from tussocks outside which *Schoenus* seedlings will survive is constant; it depends upon the intensity of the fires, which may depend upon the wind, the composition of the flora, and dryness of the litter both on and (if any) between tussocks: it also depends upon the height of the tussocks; and upon the frequency of burning in relation to the interval elapsing between germination and the time when *Schoenus* seedlings become fire-resistant; and so on. But the more numerous and close the tussocks, the more numerous and intense the fires, so in spite of the variability above it can be understood how eventually the survival of seedlings to form new tussocks may become nil, because of enforced proximity to the centres of burning.

The density of the tussock population studied has not reached this saturation value, and may never do so, for the existing *Schoenus* tussocks may become distorted and confluent or otherwise influenced by the growth of *Molinia*² at such a rate that survival of *Schoenus* seedlings in spaces in which they might otherwise have survived might be prevented, so that the tussock density would be fixed at or near the present unsaturated level.

¹ See Clapham (1936) for a discussion of the expectation of under-dispersion of vegetation units in small areas: the expectation under natural conditions is extremely small. In the data of American prairie vegetation used by him, demonstration of under-dispersion of any one species was impossible, and even random scatter was rare. Other data, both published and unpublished (by various authors) tend to the same conclusion.

² *Molinia* growth, which is favoured at the expense of that of *Schoenus* by repeated burning, is lateral as well as vertical; thus a *Molinia* tussock will grow upwards and outwards in all directions, while a *Schoenus* tussock will grow upwards only.

CONCLUSION AND SUMMARY

Schoenus in the Oxford district occupies habitats where a richly calcareous water table is kept permanently near the ground surface. Although at one time such conditions might have had a wide distribution in undrained fens in this area, they are now confined to peat cuttings (and to certain other habitats where conditions can be shown to be related and similar).

When the ground on which a *Schoenetum* forms is sloping, the rigid, persistent, vertically growing, and compact *Schoenus* peat is the only part of the soil which is able to resist water erosion; thus *Schoenus* plants grow up and form tussocks, while the soil between them does not increase (appreciably) in depth.

When the ground is level, soil-depth increase between *Schoenus* plants is not hindered, and *Schoenus* "hummocks" owe their apparent greater height almost entirely to the caespitose habit of the plant.

Colonization by *Molinia* brings into active operation the fire factor. This supplements, and increases the activity of, tussock-forming agents; it increases the susceptibility of burnt areas to burning in the future, and postpones carr invasion.

Subrandom dispersion of tussocks, statistically proved, is explained by supposing that burning of tussock vegetation causes death of *Schoenus* seedlings within a certain radius of burned tussocks, so that new tussocks spring up only outside this radius of existing ones. It is not supposed, however, nor is it necessary to suppose, that this "certain radius" is constant.

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REFERENCES

- Clapham, A. R. "Over-dispersion in grassland communities." This JOURN. 24, 232, 1936.
Clapham & Dawkins. Unpublished.

THE WEED HERBAGE OF A SLIGHTLY ACID ARABLE SOIL

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THE Permanent Wheat and Barley plots were laid down in Stackyard Field at Woburn in 1876 and carried their respective crops without intermission until 1926. In the latter year a two-year fallow was started, the plots were left entirely uncropped during this period, and they were resown with their appropriate cereal in the season 1928-9. The cropping was then continued for five years, but without any further addition of manures, and the plots were then again allowed to remain fallow for two more years. This last period of fallowing has allowed a careful study of the weed herbage which grew on the plots at various times of the year, for the land was scuffled and the weeds destroyed after about every two months during the growing season. As there was no fresh addition of manures, and no cropping, while the treatment in other respects had been and was similar, the differences in the herbage would seem to be the result of the differences in the manures during the previous fifty years. In other words, a soil has been prepared by means of the long-continued addition of manures which has, in each case, its own characters, and these are illustrated by the herbage which now grows on the land.

The whole weed-seed population of these plots has been studied by Brenchley & Warington(4) in the first fallow in 1927, by taking samples from the plots and counting the plants that appear when the soils are placed in favourable conditions for germination during about three years. These results enable the total number of seeds of each of the weeds to be ascertained, the period of the year when they most frequently germinate, and the length of time they may be expected to remain in the soil before germination. There seemed, however, a need to supplement their description by a study of the actual weeds that appeared in the field, with each previous soil treatment, at the different times of the year, and of the way in which such appearance was affected by fallowing. It has not been possible to make a study of the vegetation on as many plots as was done by Brenchley & Warington, and regular examinations and counts have been made only after ten different treatments. In addition to this, notes based on eye observations have been made at intervals throughout the period to which the present study refers, chiefly in relation to the perennial weeds. Further, only the principal weeds have been considered, and there are many which occur only rarely which have been

ignored. In some cases the species of a single genus, notably the various types of *Veronica*, have been put together.¹

As has been noted by Brenchley & Warington, the soil at Woburn is sandy, overlying pure sand. It is well drained and water may be said never to lie on it. It is naturally acid (*pH* about 6.0) and is almost free from exchangeable lime (see Crowther(5)). The acidity has naturally been very much emphasized on the plots which have been treated with sulphate of ammonia. The *direct* effect of the actual manures themselves on the weed herbage can be left out of consideration, for no manure of any sort has been added since 1926, and whatever differences were to be found in 1934 and 1935 occurred on soil which had been prepared by previous application of manures, and were not caused by the addition of the manures themselves.

The treatment of the plots which have been studied, for the first fifty years of the experiment, was as follows:

Plot no.	Treatment 1876-1926	<i>pH</i> of soil (1932) in permanent barley area
1	Unmanured	5.4
2a	Sulphate of ammonia	4.4
2b	Sulphate of ammonia with lime	5.8
3a/b	Nitrate of soda	5.6
4a	Mineral manures	5.4
4b	Mineral manures and lime	5.7
5a	Mineral manures and sulphate of ammonia	4.7
5b	Mineral manures and sulphate of ammonia with lime	5.9
6	Mineral manures and nitrate of soda	5.8
11b	Farmyard manure	5.8

The figures on which the present study of the annual weeds is based were obtained in the following manner in the permanent barley area only. Quadrats of 1 ft. sq. were taken, more or less at random, in different parts of each plot studied, and every weed in each quadrat was examined and counted. Three or, more usually, four such quadrats were taken on each plot at each set of observations and the whole number of each species was added together as representative of that plot. All sizes of each plant were given equal value and counted each as one. In the years of critical observation, that is to say, during the years 1934 and 1935, when the plots were fallow, the counts were made just before each scuffling of the ground to kill each lot of weeds. Such counts were, therefore, taken on the following dates:

1934: (1) 25 April.	1935: (1) 21 March.
(2) 14 June.	(2) 11 May.
(3) 23 July.	(3) 27 June.
(4) 20 September.	(4) 15 September.
(5) 27 November.	

¹ It is recognized that this putting together of the several species of *Veronica* is unwise, as their habits are substantially different, but the conditions of enumeration prevented their separation.

These observations were supplemented by observations in 1936 just before the barley crop was sown (4/5 March), once during the growth of that crop, and finally once after that crop was removed (16 Sept.). The observations on the perennial weeds were made by the eye throughout the whole of the period of study.

ANNUAL WEEDS

A. The general character of the weed herbage

The actual species of annual weeds to be found in the land now under consideration have been indicated by Brenchley & Warington(4). Their method gave an opportunity for practically all the seeds present in the land to germinate during a period of three years. In the present tests, on the other hand, the number obtained represented only those which happened to be in a favourable situation for germination in the field at some time during the period when the counts were made. But a comparison between their findings in 1927 and the present results may be instructive. The order of frequency, taking the permanent barley area as a whole, is shown in the following table. This table, however, only deals with the more common species, but it includes all the important weeds which grew in the three years 1934, 1935 and 1936. In 1936, the complete enumeration could only be done up to the time when the barley crop was well above the ground. Another count was made after harvest, and this is included, though it may possibly contain a few plants from seeds deposited in the same year. Apart from these few, the figures may be taken to represent the weed seeds which were in the soil at the beginning of 1934, that is to say before the commencement of the fallow, and which germinated up to the harvest of 1936. I have also included the total number of weeds found by Brenchley & Warington in the beginning of 1927, before the commencement of the first fallow.

Total weeds in permanent barley soil per square yard

	Brenchley 1927	Mann			Total
		1934	1935	1936	
<i>Spergula arvensis</i>	16,722	1232	1879	586	3697
<i>Capsella bursa-pastoris</i>	1,578	21	25	5	51
<i>Polygonum aviculare</i>	1,366	110	17	95	322
* <i>Poa annua</i>	1,364	115	93	80	288
<i>Stellaria media</i>	950	66	75	41	182
<i>Gnaphalium uliginosum</i>	1,045	1	76	27	104
<i>Veronica</i> sp.	1,036	59	101	36	196
<i>Matricaria inodora</i>	243	838	504	329	1671
<i>Lamium amplexicaule</i>	192	3	7	2	12
<i>Chenopodium album</i>	168	5	2	5	12
<i>Senecio vulgaris</i>	87	9	8	7	24
<i>Alchemilla arvensis</i>	46	4	0	1	5
<i>Polygonum convolvulus</i>	31	1	1	3	5
<i>Vicia hirsuta</i>	—	6	4	1	11
Others	—	9	18	7	34
Total	24,828				6614

* In the enumerations in 1934, 1935 and 1936 a strict separation of the grasses was not made. *Poa annua* is so completely dominant among grasses that it is probable the error thus introduced is not very great.

The above include all the annual weeds which are of importance and they are arranged in approximately the order of frequency in which they were found by Brenchley & Warington, in the permanent barley area as a whole. It will be seen that, in general, the order which I have now found differs only in details from that found by Brenchley & Warington seven years earlier, except in one or two important respects. The most striking of these is the enormous increase in the amount of *Matricaria inodora* (mayweed) both relatively and absolutely. This weed, which is known to flourish exceedingly when there is plenty of light, is particularly common in sparse crops, such as the barley crops have been between 1929 and 1933. When this is coupled with not very thorough intercultivation of the barley crop during these years, its increase is explained.

The numbers of other weeds which I have collected from the field during three years are much less than Brenchley & Warington were able to obtain when the soil was put into the most favourable conditions for germination. Even if the total weed seeds contained in the soil was the same in number, this lower enumeration would be expected, but the degree to which the number is lower is shown in the following table. The table also shows the proportion of the named weeds, actually found in each case, which consists of each species.

	No. of plants growing in the field in 1934-6 as percentage of total number in 1927	Percentage of the named weeds found of each species	
		1927	1934-6
<i>Spergula arvensis</i>	23.0	67.3	56.1
<i>Capsella bursa-pastoris</i>	3.4	6.4	0.8
<i>Polygonum aviculare</i>	23.6	5.5	4.9
<i>Poa annua</i>	22.0	5.4	4.4
<i>Stellaria media</i>	19.9	3.8	2.7
<i>Gnaphalium uliginosum</i>	10.3	4.2	1.6
<i>Veronica</i> sp.	19.6	4.2	3.0
<i>Matricaria inodora</i>	714.1	1.0	25.3
<i>Lamium amplexicaule</i>	6.5	0.8	0.2
<i>Chenopodium album</i>	7.4	0.7	0.2
<i>Senecio vulgaris</i>	28.6	0.4	0.4
<i>Alchemilla arvensis</i>	11.4	0.2	0.1
<i>Polygonum convolvulus</i>	16.7	0.1	0.1
<i>Vicia hirsuta</i>	?	—	0.2
Total (of above species)	26.5	100.0	100.0

The proportion of the weeds which I found on the field in 1934-6 to those found by Brenchley & Warington was in the mean 26.5%, or a little above one-quarter. As already stated, the increase of the *Matricaria* is prodigious. All the other weeds have fallen off more than the total, with the exception of *Senecio vulgaris*, and some of them remarkably so. This is very noticeable with *Capsella*, *Lamium* and *Chenopodium*. The *Vicia hirsuta*, which has become a very important weed, was absent on this barley ground in 1927.

B. *Periodicity of the weeds*

As it was necessary in the present series of counts in the field to accommodate oneself to the requirements of the farming system, it has not been possible to determine the numbers of each weed which grew between fixed dates. But generally speaking, the attempt was made to count the weeds, during the fallow, once during the first quarter of the year, once or twice during the second quarter, once or twice during the third quarter, and once during the last quarter of the year. The table on p. 94 shows the numbers of each weed, taking the plots as a whole, which have been found at each count in each year. Unfortunately no count was made in the last quarter of 1935 or of 1936. In 1936 this is not of great importance, as no provision against reinfection could be made in that year owing to the presence of a barley crop. All the figures given are from all the plots listed on p. 90, except those on the first date, on 25 April 1934, which was taken on Plots 1, 2a, 6, and 11b only.

The time at which the great majority of each species of weed appear in the field is well shown by the above table. It must be remembered that the first set of figures in 1934 represents the whole growth between 7 November 1933 when the land was scuffled and 25 April 1934. It contains, therefore, all the winter and early spring growing weeds. The very great proportion of the total number of the most important weeds growing during the year which germinate before 25 April is shown by the following figures representing the percentage of the total number in 1934 which were found on 25 April.

	%
<i>Spergula arvensis</i>	10
<i>Matricaria inodora</i>	55
<i>Polygonum aviculare</i>	52
<i>Stellaria media</i>	38
<i>Veronica</i> sp.	37
<i>Vicia hirsuta</i>	67

It is quite clear that with most of the important annual weeds on this soil, roughly half the year's growth of plants have germinated before the end of April, and that, of these, a very large proportion germinate in the last month of the period. It would suggest that, so far as destruction of annual weeds is concerned, a thorough harrowing or scuffling of the land at the end of April is very effective and very much more so than at the end of March.

What has been said does not apply to all the important weeds. Spurrey (*Spergula arvensis*) is an example, for it seems to germinate pretty regularly throughout the year and seems to be in a condition to germinate whenever the seed has lost its dormancy and the weather conditions are favourable. With *Matricaria inodora*, and the grass, *Poa annua*, after the spring burst, there continues a very steady amount of germination during the rest of the season, even during the last quarter (as judged by the 1934 figures). The same is also true of the several *Veronicas* which are found in this field.

The position is quite different with *Polygonum aviculare*, the third most frequent weed on this land. This has almost finished germination by the middle of May, as the following figures for 1935 show:

Polygonum aviculare

Plants germinated per square yard between:

(1) 27 Nov. 1934 and 20 Mar. 1935	3.5
(2) 20 Mar. 1935 and 10 May 1935	109
(3) 10 May 1935 and 26 June 1935	5
(4) 26 June 1935 and 14 Sept. 1935	0

With this weed, therefore, it would appear that almost all the seeds germinate in the field in the spring, and, in the present case, between 20 March and 10 May. The actual dates would, of course, be affected by the particular weather in any year.

A similar result was obtained in 1936, when *no* plants were found on 4 March, no less than 68 per square yard on 11 May, and 27 per square yard for the later period up to 16 September.

Another weed whose behaviour is peculiar is *Gnaphalium uliginosum*, the marsh cudweed. Brenchley & Warrington found that when the Woburn soil was placed in favourable conditions for germination "the majority of the seeds germinated at once, but a few seedlings appeared fairly regularly over the next two years". In the field, on the other hand, this very frequent weed is as seasonal as any that exist, and, moreover, it appears to be able to stay in the soil for more than one year without germination. Thus, in 1934, there were hardly any weeds of this species on any of the plots. In 1935, on the other hand, they were abundant, the numbers per square yard at the several counts being shown in the following table.

Gnaphalium uliginosum

(1) Plants found on 20 Mar. 1935	None
(2) " " 10 May 1935	None
(3) " " 26 June 1935	62
(4) " " 14 Sept. 1935	14
(1) " " 4 Mar. 1936	None
(2) " " 11 May 1936	None
(3) " " 16 Sept. 1936	27

In 1936 the count in September would include the same period as in the last two counts of 1935.

Still another weed is interesting from the present point of view, namely *Chenopodium album*. Under the conditions favourable to germination provided by Brenchley & Warrington, practically all the viable seeds of this weed germinated in the first quarter the experiment was running. Far different is the state of affairs in the field, though the actual number of specimens of this weed found was only small. In 1934, no seeds of this weed had germinated by

25 April and after that date the number found on various dates is shown in the following table.

Chenopodium album

(1)	Plants found on	14 June 1934	1.9
(2)	" "	23 July 1934	2.6
(3)	" "	19 Sept. 1934	None
(4)	" "	27 Nov. 1934	None
(1)	" "	20 Mar. 1935	None
(2)	" "	10 May 1935	None
(3)	" "	26 June 1935	1.8
(4)	" "	14 Sept. 1935	0.4
(1)	" "	4 Mar. 1936	None
(2)	" "	11 May 1936	3.6
(3)	" "	16 Sept. 1936	0.2

It seems clear that almost all the germinations of the seeds of this weed have taken place, in each year, in either May or June.

D. Effect of fallow on weed herbage

The land, as already stated, remained without a crop during the whole of the years from the harvest of 1933 to the sowing time of 1936. It was kept well cultivated during this time, and there must have been very little seeding of the weeds during that period. The actual cultivation on the land done during this time was as follows:

1933	
21-26 Aug.	Tractor ploughed
30 Aug.	Tractor cultivated
7-8 Sept.	" "
30 Sept.	" "
17-18 Oct.	Tractor ploughed
7-8 Nov.	Tractor cross-cultivated
1934	
25 April	Tractor cultivated
2 May	Tractor cultivated and harrowed
11-12 May	Tractor harrowed and rolled
14-15 June	Tractor cultivated and harrowed
26 June	Tractor cross-cultivated
7-8 Aug.	Harrowed
25 Sept.	Tractor cultivated
1 Oct.	" "
30 Nov. to 12 Dec.	Tractor ploughed
1935	
22 Mar.	Tractor cultivated and harrowed
26 Mar.	Tractor cultivated
28 Mar.	Tractor harrowed and rolled
30 Mar.	Tractor " "
13 May	Tractor cultivated
22 May	" "
28 June	Tractor cultivated and harrowed
2 July	" "
19-26 Sept.	Tractor ploughed
1936	
10-13 Mar.	Ploughed with one way plough
17 Mar.	Double harrowed
19 Mar.	Double harrow and drill barley
20 Mar.	Double harrowed
25 Mar.	Cambridge rolled
13 May	Harrowed
20 May	" "
26 May	" "

In spite of this intensive treatment, it is recognized that there would be danger of certain of the weeds, notably *Veronicas*, *Capsella* and *Stellaria*, seeding during the winter between November and March or April, when no cultivation was done. There would, therefore, be the chance of the weeds reinfesting the land during the progress of the fallow, and to this extent the figures given below will be open to criticism. It is probable, however, that the error so introduced is a small one and that the relative number of seedlings in the successive seasons will be some measure, at any rate, of the success of the fallowing operation in getting rid of these annual weeds.

The natural way of instituting such a comparison would be to take the relative number of plants of each weed in the successive years, but it is not quite certain how far the figures allow this to be done. The autumn numbering was missed in 1935 and in 1936, and thus, to make any comparison we must also only take the first three quarters of the year 1934. If we do this, the relative numbers of each weed are shown in the following table:

Effect of fallowing on number of weeds

	1934	1935		1936	
		No.	Reduction on 1934 %	No.	Reduction on 1934 %
Weeds per square yard					
<i>Spergula arvensis</i>	820	1879	Inc.	586	28.5
<i>Matricaria inodora</i>	563	504	10.5	329	41.6
<i>Poa annua</i>	82	93	Inc.	80	2.4
<i>Stellaria media</i>	34	75	Inc.	41	Inc.
<i>Veronica</i> sp.	41	101	Inc.	36	12.2
<i>Polygonum aviculare</i>	109	117	Inc.	95	12.8
<i>Gnaphalium uliginosum</i>	0	76	Inc.	27	Inc.
<i>Capsella bursa-pastoris</i>	21	25	Inc.	5	76.2
<i>Chenopodium album</i>	5	2	60.0	5	Nil
<i>Senecio vulgaris</i>	9	8	11.0	7	22.2
<i>Polygonum convolvulus</i>	1	1	Nil	3	Inc.
<i>Lamium amplexicaule</i>	3	7	Inc.	2	33.3
<i>Vicia hirsuta</i>	6	4	33.3	1	83.3
<i>Alchemilla arvensis</i>	4	0	100.0	1	75.0

Judged by these figures, the effect of the fallow in getting rid of annual weeds is very disappointing. As regards the worst weed of this ground, *Spergula arvensis*, a definite reduction was not apparent till the second year. Mayweed (*Matricaria inodora*) was certainly reduced slightly in the first year, and by over 40% in the second year. The annual grass, *Poa annua*, was practically unaffected, and this agrees with eye observation on these plots. A very substantial reduction in the amounts of *Veronica* sp. and *Polygonum aviculare* was found in the second year and a similar effect seems to be clear with some of the less common weeds, though the numbers are so small that great stress cannot be laid upon them. *Alchemilla arvensis* seems to have been almost eradicated from the area, as judged by eye observation. On the other hand, *Vicia hirsuta*, appeared in fair amount in the barley crop of 1936 in spite of its apparent reduction as shown by these figures.

Of the common weeds, therefore, the two-year fallow has been fairly successful in reducing the amount of *Spergula arvensis* (28.4%), *Matricaria inodora* (41.6%), *Veronica* (12.2%), *Gnaphalium uliginosum* (12.8%), and *Capsella bursa-pastoris* (76.2%). It has apparently had no effect on *Stellaria media* or *Poa annua*. This result is disappointing, for two years is as much as it is possible usually to give for a fallow and if the reduction in annual weeds is so slow it hardly seems an economical method of trying to get rid of them. The effect on perennial weeds will be discussed later.

Spergula arvensis is so completely the dominant weed in all these plots that it is interesting to compare the effect of the fallow on the proportion of this weed to the total annual herbage in each of the three years for which the records were taken. These show that this proportion was reduced in the last year. The actual figures were as follows:

Proportion of total annual weeds composed of Spergula

	%
1934	60.0
1935	61.6
1936	45.6

We know from the work of Brenchley & Warington that *Spergula* is able to remain for several years ungerminated in the soil; these figures seem to show that other weeds possess the same property to at least the same extent.

E. Effect of previous manurial treatment on the weed herbage

So far we have dealt with the weed herbage of the permanent barley area as a whole. But it is at once clear on looking over the ground that the plots examined (see p. 90) differ considerably not so much in the character of the weeds as in their proportion to one another. Brenchley & Warington have stated (4) that the association of specific weeds with certain manures is not nearly so marked here as in the corresponding Rothamsted plots, as practically all the major species occur to some extent on most of the plots. But there are a number of interesting points which have come out of my observations.

The chief interest perhaps lies in the distribution of the dominant weed, namely, *Spergula arvensis*. Though this is the most important weed on all plots, yet the proportion which it forms of the total herbage varies greatly. The following table shows the total number of annual weeds counted in the three years for each plot observed, the number of these weeds that consisted of spurrey, and the proportion that the latter bore to the total weeds. I have added a statement of the proportion that was found on the same plots by Brenchley & Warington in 1927.

Weeds found on each selected plot from 1934 to 1936

Plot	Treatment	pH of soil	Total weeds per square yard 1934-6			Percentage of <i>Spergula</i>	1927 percentage of <i>Spergula</i> (Brenchley & Warrington)
			Total	<i>Spergula arvensis</i>	(Others)		
1	Nothing	5.4	3184	1295	1889	40.7	49.3
2a	Sulphate of ammonia only	4.4	7669	7346	323	95.8	96.4
2b	Sulphate of ammonia and lime	5.8	5050	2957	2093	58.6	50.9
3a/b	Nitrate of soda	5.6	6228	3086	3142	49.5	59.6
4a	Mineral manures	5.4	3236	1169	2067	36.1	35.5
4b	Mineral manures and lime	5.7	4792	2160	2632	45.1	52.7
5a	Mineral manures and sulphate of ammonia	4.7	8183	7378	805	90.2	91.1
5b	Mineral manures and sulphate of ammonia and lime	5.9	4874	2782	2092	57.1	56.8
6	Mineral manures and nitrate of soda	5.8	6409	2885	3524	45.0	38.5
11b	Farmyard manure	5.8	8051	4743	3308	58.9	30.0

The relationship of the number of plants of *Spergula* to the acidity of the soil is very well shown, for in both Brenchley's and my own observations, this weed forms over 90% of the total herbage in both of the plots made acid by the use of sulphate of ammonia, whether mineral manures have been employed or not. Further, not only is the proportion greatest, but the absolute number of *Spergula* plants per unit area is the greatest. There is a clear result from these figures that both the absolute and relative frequency of *Spergula* appears to decrease rapidly as the pH value of the soil goes from 4.4 to 5.4, but, as it becomes still less acid, there is no further reduction in either its absolute or relative amount. If the frequency of the *Spergula* is shown in relation to the pH value, the result just referred to is indicated.

Relation of prevalence of Spergula to soil acidity

pH value	No. of <i>Spergula</i> plants per square yard	Total weeds per square yard	Proportion of total weeds (%)
4.4	7436	7669	95.8
4.7	7378	8183	90.2
5.4	1232	3210	38.3
5.6	3086	6228	49.5
5.7	2160	4792	45.1
5.8	3528	6503	54.3
5.9	2782	4874	57.1

The effect of mineral manures, as such, does not seem apparent, and, though the total number of weeds (and of *Spergula*) is higher on the plot which formerly received farmyard manure, yet the proportion of *Spergula* is very little affected. The following table shows this.

*Weed herbage of a slightly acid arable soil**Relation of prevalence of Spergula to mineral manures*

Manurial treatment	No. of <i>Spergula</i> plants per square yard	Total weeds per square yard	Proportion of <i>Spergula</i> in total weeds %
No mineral manures	3671	5533	66.4
Mineral manures	3275	5499	59.5
Farmyard manure	4743	8051	58.5

The effect of the addition of lime is of still more interest. We have three cases in which we can compare adjacent plots, limed and unlimed.

Relation of prevalence of Spergula to liming

Manurial treatment	No. of <i>Spergula</i> plants per square yard	Total weeds per square yard	Proportion of <i>Spergula</i> in total weeds %
Sulphate of ammonia:			
(a) Without lime	7346	7669	95.8 (pH 4.4)
(b) With lime	2957	5050	58.6 (pH 5.8)
Sulphate of ammonia and mineral manures:			
(a) Without lime	7378	8183	90.2 (pH 4.7)
(b) With lime	2782	4874	57.1 (pH 5.9)
Mineral manures only:			
(a) Without lime	1169	3236	36.1 (pH 5.4)
(b) With lime	2160	4792	45.1 (pH 5.7)

The effect of lime seems almost entirely to be due to its effect on the acidity of the soil. In the case of the plots merely treated with mineral manures, which have never become very acid, its effect is small and is not in the direction of reducing either the absolute or the relative amount of spurrey.

The permanent effects of the other treatments seem very small.

In considering the relation between the former manurial treatment of the soil and the other weeds, we must take the figures after the subtraction of the number of *Spergula* plants, or else the difference will be swamped. If we do this, immediately *Matricaria inodora* stands out as the principal weed on almost all the plots. Its subdominant position is shown almost everywhere.

Matricaria inodora on each selected plot from 1934 to 1936

Plot	Treatment	pH of soil	Weeds per square yard other than <i>Spergula arvensis</i> , 1934-6		
			Total	<i>Matricaria</i> <i>inodora</i>	Percentage of <i>Matri-</i> <i>caria</i>
1	Nothing	5.4	1889	1283	67.9
2a	Sulphate of ammonia only	4.4	323	25	7.7
2b	Sulphate of ammonia and lime	5.8	2093	1372	65.6
3a/b	Nitrate of soda	5.6	3142	2327	74.1
4a	Mineral manures	5.4	2067	1537	74.3
4b	Mineral manures and lime	5.7	2632	1337	50.8
5a	Mineral manures and sulphate of ammonia	4.7	805	85	10.6
5b	Mineral manures and sulphate of ammonia and lime	5.9	2092	883	42.2
6	Mineral manures and nitrate of soda	5.8	3524	1924	54.7
11b	Farmyard manure	5.8	3308	1283	38.8

We may consider the relationship of the prevalence of *Matricaria inodora*, both absolutely and relatively, to the acidity, to the presence of mineral manures (phosphates and potash), and to the previous addition of lime, after eliminating the *Spergula*, as noted above. The results are as follows:

Relation of prevalence of Matricaria inodora to soil acidity

pH value	No. of <i>Matricaria</i> plants per square yard	Total weeds per square yard	Proportion of <i>Matricaria</i> to total weeds (without spurrey) %
4.4	25	323	7.7
4.7	85	805	10.6
5.4	1410	1978	71.2
5.6	2327	3142	74.1
5.7	1337	2632	50.8
5.8	1526	2975	51.3
5.9	883	2092	42.2

Here we see an acid-loving weed, provided the acidity is not much greater than that represented by a pH value of 5.4–5.6. When the acidity becomes less than this, the absolute and relative abundance of the weed rapidly decreases.

The relation of the weed to the previous addition of mineral manures (phosphates and potash) is shown in the following table.

Relation of prevalence of Matricaria to mineral manures

Manurial treatment	No. of <i>Matricaria</i> plants per square yard	Total weeds per square yard	Proportion of <i>Matricaria</i> to total (less spurrey) %
No mineral manures	1252	1862	67.2
Mineral manures	1153	2224	51.9
Farmyard manure	1283	3308	38.8

It is clear that the application of mineral manures for the first fifty years of this experiment has not appreciably affected the number of *Matricaria* plants which now appear in the course of three years. The mineral manures, and even more so, the farmyard manure, have increased the total amount of weed herbage (other than spurrey) and so decreased the proportion represented by the *Matricaria*.

The effect of the addition of lime may also be shown.

Relation of prevalence of Matricaria to liming

Manurial treatment	No. of <i>Matricaria</i> plants per square yard	Total weeds per square yard	Proportion of <i>Matricaria</i> in total weeds (without spurrey) %
Sulphate of ammonia:			
(a) Without lime	25	323	7.7 (pH 4.4)
(b) With lime	1372	2093	65.6 (pH 5.8)
Sulphate of ammonia and mineral manures:			
(a) Without lime	85	805	10.6 (pH 4.7)
(b) With lime	883	2092	42.2 (pH 5.9)
Mineral manures only:			
(a) Without lime	1537	2067	74.3 (pH 5.4)
(b) With lime	1337	2632	50.8 (pH 5.7)

It would seem clear that there is little specific effect of the lime. The whole of the above differences both in respect to the absolute and the relative amount of *Matricaria* in the non-spurrey herbage can be explained by reference to the pH value of the soil.

We may apply a similar method of treatment to some of the other weeds, giving the total number of each and the proportion to the total weeds, less the *Spergula* and the *Matricaria*. The exclusion of the two dominant weeds is necessary as otherwise the relationships are entirely swamped by the influence of the two above.

Poa annua

We may first consider the prevalence of annual grass, almost entirely *Poa annua*. The latter is so completely dominant among the grasses that we may take all the plants of grass that were counted as belonging to this species.

A. Relation of prevalence of *Poa annua* to soil acidity.

pH value	No. of <i>Poa</i> plants per square yard	Total weeds per square yard	Proportion of <i>Poa annua</i> to total weeds %
4.4	129	298	43.3
4.7	329	720	45.7
5.4	154	564	27.2
5.6	112	815	13.7
5.7	157	1295	12.2
5.8	343	1449	23.7
5.9	179	1209	14.8

B. Relation of prevalence of *Poa annua* to mineral manures.

Manurial treatment	No. of <i>Poa</i> plants per square yard	Total weeds per square yard	Proportion of <i>Poa annua</i> to total weeds %
No mineral manures	194	610	31.8
Mineral manures	264	1069	24.7
Farmyard manure	346	2025	17.1

C. Relation of prevalence of *Poa annua* to liming.

Manurial treatment	No. of <i>Poa</i> plants per square yard	Total weeds per square yard	Proportion of <i>Poa annua</i> to total weeds %
Sulphate of ammonia:			
(a) Without lime	129	298	43.3 (pH 4.4)
(b) With lime	171	721	23.7 (pH 5.8)
Sulphate of ammonia and mineral manures:			
(a) Without lime	329	720	45.7 (pH 4.7)
(b) With lime	179	1209	14.8 (pH 5.9)
Mineral manures only:			
(a) Without lime	145	523	27.7 (pH 5.4)
(b) With lime	157	1295	12.2 (pH 5.7)

The figures for *Poa annua* are of considerable interest. This grass is one of the few weeds that can flourish on soil as acid as those which have been treated for fifty years with sulphate of ammonia. In these cases the weed herbage is of a very simple character, so far, at any rate, as annual weeds are concerned.

Once *Spergula* has been excluded, almost the whole annual weed herbage at the acidity of pH 4.4 consists of *Poa* and *Polygonum aviculare* (see below). In other cases the amount of this grass does not vary to a very great extent in absolute amount, though the proportion gets less as other weeds are encouraged by the mineral manure and farmyard manure applications. The effect of the liming of the land on the absolute abundance of this grass seems very small.

Polygonum aviculare

The next most frequent weed on the area we are considering is *Polygonum aviculare*. This is a weed which seems very little affected by the previous manurial treatment of the land. Further, it seems to grow quite without difficulty on the most acid of the soils with which we are dealing, and in such acid soils it, with *Poa annua*, almost forms the whole of the annual weed growth, apart from spurrey.

The actual effects of differing conditions are shown in the following tables.

A. *Relation of prevalence of Polygonum aviculare to soil acidity.*

pH value	No. of <i>Polygonum</i> plants per square yard	Total weeds per square yard	Proportion of <i>Polygonum</i> to total weeds %
4.4	125	298	41.9
4.7	343	720	47.6
5.4	121	564	21.5
5.6	237	815	29.1
5.7	307	1295	23.8
5.8	295	1449	20.3
5.9	140	1209	11.6

B. *Relation of prevalence of Polygonum aviculare to mineral manure.*

Manurial treatment	No. of <i>Polygonum</i> plants per square yard	Total weeds per square yard	Proportion of <i>Polygonum</i> to total weeds %
No mineral manures	177	610	29.0
Mineral manures	261	1069	24.4
Farmyard manure	267	2025	13.2

C. *Relation of prevalence of Polygonum aviculare to liming.*

Manurial treatment	No. of <i>Polygonum</i> plants per square yard	Total weeds per square yard	Proportion of <i>Polygonum</i> to total weeds %
Sulphate of ammonia:			
(a) Without lime	125	298	41.9
(b) With lime	220	721	30.5
Sulphate of ammonia and mineral manures:			
(a) Without lime	343	720	47.6
(b) With lime	140	1209	11.6
Mineral manures only:			
(a) Without lime	116	523	22.2
(b) With lime	307	1295	23.8

This weed is, therefore, one of the most indifferent of all weeds to changes in the condition of the soil. It is at all times one of the most common weeds

on this land, and is comparatively little affected by the soil becoming acid, by liming, or even by the addition of mineral manures, though, in this latter case, there is some increase with the manuring.

Gnaphalium uliginosum

In dealing with the occurrence of *Gnaphalium* in the Woburn soil, Brenchley & Warington call attention to the apparent preference for land treated with sulphate of ammonia and mineral manures. This weed is present in fair amount on most of the plots, and the present study enables us to consider further whether the supposed preference is a real one. The following tables show the results in the same way as in previous cases.

A. *Relation of prevalence of Gnaphalium to soil acidity.*

pH value	No. of <i>Gnaphalium</i> plants per square yard	Total weeds per square yard	Proportion of <i>Gnaphalium</i> to total weeds %
4.4	27	298	9.1
4.7	9	720	1.2
5.4	116	564	20.6
5.6	87	815	10.7
5.7	117	1295	9.1
5.8	144	1449	9.9
5.9	123	1209	10.2

B. *Relation of prevalence of Gnaphalium to mineral manures.*

Manurial treatment	No. of <i>Gnaphalium</i> plants per square yard	Total weeds per square yard	Proportion of <i>Gnaphalium</i> to total weeds %
No mineral manures	82	610	13.4
Mineral manures	107	1069	10.0
Farmyard manure	173	2025	8.6

C. *Relation of prevalence of Gnaphalium to liming.*

Manurial treatment	No. of <i>Gnaphalium</i> plants per square yard	Total weeds per square yard	Proportion of <i>Gnaphalium</i> to total weeds %
Sulphate of ammonia:			
(a) Without lime	27	298	9.1
(b) With lime	77	721	10.7
Sulphate of ammonia and mineral manures:			
(a) Without lime	9	720	1.2
(b) With lime	123	1209	10.2
Mineral manures only:			
(a) Without lime	94	523	17.8
(b) With lime	117	1295	9.1

The addition of sulphate of ammonia and mineral manures has no specific advantage for this weed. It apparently dislikes a soil more acid than is represented by a pH value of 5.4; with less acidity than this, there seems very little difference in the treatment on the absolute number of *Gnaphalium* which have grown.

Stellaria media and Veronica sp.

The remaining weeds may be dealt with more shortly, though the two now under discussion are among the most common on the area. In the case of *Veronica*, I have put together all the plants of this genus and have not distinguished between the three species which occur on the area under study. Both *Veronica* and *Stellaria* are, however, very sensitive to acidity greater than a certain point, and almost disappear in the plots more acid than a pH value of 5.4.

The relationship with the acidity, with the addition of mineral manures, and with the addition of lime are shown in the attached table.

A. *Relation of prevalence of Stellaria and Veronica to soil acidity.*

pH value	No. of <i>Stellaria</i> plants per square yard	No. of <i>Veronica</i> plants per square yard	Total weeds	Proportion of	
				<i>Stellaria</i> to total weeds %	<i>Veronica</i> to total weeds %
4.4	9	4	298	3.1	1.3
4.7	—	—	720	?	?
5.4	92	65	564	16.3	11.5
5.6	112	27	815	13.7	3.3
5.7	301	145	1295	23.3	11.2
5.8	265	253	1449	18.3	17.4
5.9	261	354	1209	21.6	29.3

B. *Relation of prevalence of Stellaria and Veronica and mineral manures.*

Manurial treatment	No. of <i>Stellaria</i> plants per square yard	No. of <i>Veronica</i> plants per square yard	Total weeds	Proportion of	
				<i>Stellaria</i> to total weeds %	<i>Veronica</i> to total weeds %
No mineral manures	65	50	610	10.7	8.2
Mineral manures	327	136	1069	30.6	12.7
Farmyard manure	471	536	2025	23.3	26.5

C. *Relation of prevalence of Stellaria and Veronica to liming.*

Manurial treatment	No. of <i>Stellaria</i> plants per square yard	No. of <i>Veronica</i> plants per square yard	Total weeds	Proportion of	
				<i>Stellaria</i> to total weeds %	<i>Veronica</i> to total weeds %
Sulphate of ammonia:					
(a) Without lime	9	4	298	3.1	1.3
(b) With lime	97	98	721	13.5	13.6
Sulphate of ammonia and mineral manures:					
(a) Without lime	—	—	720	—	—
(b) With lime	261	354	1209	21.6	29.3
Mineral manures only:					
(a) Without lime	49	58	523	9.4	11.1
(b) With lime	301	145	1295	23.3	11.2

The almost complete disappearance of both these weeds in the most acid plots is very striking, but at all pH values above 5.7 there was little difference

in the amount of *Stellaria*, while the amount of *Veronica* increased right up to the least acid of the series of plots at 5.9. They are both encouraged by the presence of mineral manures, and still more by the long continued use of farmyard manure. The effect of lime, apart from the raising of the pH value, does not seem very marked.

Other weeds

There does not seem any need to deal with other weeds than the above in the same detail. The prevalence of *Capsella* seems to be very much less than in samples from the same plots eight years before. It is now almost always found on every plot, but is certainly not so prevalent as in the remainder of the field under ordinary farming. Groundsel (*Senecio vulgaris*) occurs everywhere, but, except in the plots 2b and 5b where lime has been used in conjunction with sulphate of ammonia, the amount is not large. *Chenopodium album* is only at all prevalent on the farmyard manure plot.

One of the most interesting and important weeds on this land is the wild vetchling, *Vicia hirsuta*. This weed, which was not found at all in the permanent barley land by Brechley & Warrington, is now occurring in fair amount, as was seen in the barley crops of 1937 after the present observations were complete. But, in the adjoining permanent wheat plots, it has become a veritable curse, and has not been reduced appreciably by the two years' fallow that has been given in 1934-6. It was in the latter area that it was already found by Brechley & Warrington in 1927. I was not able to get a numerical measure of its prevalence, but the notes that I made during the last two seasons may be interesting. This weed never appeared on the more acid plots, i.e. those which had a pH value of under 5.4. At first it was almost exclusively found on plots 6 and 9 (nitrate of soda and mineral manures), and plot 11b (farmyard manure) and it was quite clear that it was from these plots that any further spread took place. The two years' fallow seemed to have little effect on its prevalence. It hardly at all occurred in the plots to which mineral manures had not been applied during the whole course of the experiment. It was completely absent on plots with a pH value below 5.0, and flourished abundantly where the pH value was 5.6-5.9. Between these two values, the amount of vetchling was small but tended to increase. Inasmuch as this weed ruins, as a bindweed, the crop of wheat, and as its arrangements for the scattering and distribution of its seeds are very efficient, it is one of the most serious weeds of the area but very much more so in autumn-sown wheat than in spring-sown barley.

PERENNIAL WEEDS

So far I have dealt with the annual weeds of these soils which have been under barley with different manuring for so many years. But of at least equal importance are the perennial weeds which have appeared and which have established themselves on the plots in question. It is, however, extremely

difficult to give figures which will show their frequency, and we have to depend much more on eye observation of the position in regard to them on the different plots both before and after the fallows. As some of them are of great interest and as they have become, in a number of cases, an important factor in the success of the crop, it may be of value if some of the observations that have been made are here noted.

The perennial weeds of any importance which I have noticed on either the wheat or the barley plots for the last ten years, are the following:

- (1) *Holcus mollis*.
- (2) *Agrostis stolonifera*.
- (3) *Rumex acetosella*.
- (4) *Equisetum arvense*.
- (5) *Tussilago farfara*.
- (6) *Convolvulus arvensis*.
- (7) *Thistles*.

It is clear that these can be of great importance, and, in fact one of the reasons which is often given for the avoidance of continuous corn cropping is that it is difficult under such circumstances to prevent the land getting infested with many such weeds. This is said to be particularly the case when autumn-sown wheat is grown continuously, as the time which elapses between one crop and another is not enough to do any adequate cleaning of the ground. I will deal with the observations made on the above weeds, separately.

Holcus mollis and *Agrostis stolonifera*

The grasses with creeping rootstocks, otherwise known as *couch* grasses or *twiches*, form such a very large and important section of the really injurious weeds, that their study on land of this sort becomes a very important one. It is natural that under the long continued cultivation of corn, whether autumn or spring sown, there will be a tendency for such grasses to flourish and to increase. With a medium or heavy loam, the grass which prevails under such condition is usually *Agropyrum repens*, often known as "the true couch", but others are often found, and in some districts *Agrostis vulgaris* is said to be far the more prevalent kind of twitch. But in light land, like that which we are now considering, the former of these appears to be wholly absent, and the latter seems to be entirely replaced by *A. stolonifera*, and in some cases by *A. nigra*.

On the greensand area in which Woburn lies, however, perhaps the most serious twitch, though not the most common, is *Holcus mollis* which, though it is often hardly recognized as a twitch, really forms a very common plant in the arable areas. That it has been long recognized as a serious pest in this region is shown by notes on it in the early parts of the last century. In 1808 Batchelor(1) states that, so far as the light soils of Bedfordshire are concerned,

"the creeping soft grass (*H. mollis*) is by far the most common in such situations". Sinclair(7), in 1824, dealing with the grasses in the neighbourhood of Woburn, speaks of *H. mollis* as follows: "The roots, when once in possession of the soil, can hardly be expelled without great labour and expense. It is the true couch of light sandy soils. I have found roots 5 ft. in length, the growth of a few months only." He states further that the roots when ground up have the flavour of new made meal and that pigs are very fond of the creeping roots and "dig them up with eagerness", while he considers that the only way of getting rid of the weed is to apply yearly "sufficient dressings of clay, perhaps fifty loads per acre, till the texture of the soil is changed to a sandy loam".

When the present observations were commenced, this form of twitch had taken possession of certain plots of the permanent wheat land, and occurred also in corresponding plots in the permanent barley. This was in 1929, and it had occurred in spite of the fallow which had been carried out in 1927 and 1928. Though *H. mollis* was found on many plots, it became a complete menace only in the plots which were very acid, and then only on the wheat plots, while it was only of moderate importance on those which had been under barley.

On the wheat plots, however, where the pH value of the soil was about 4.8 or below, *H. mollis* grew with very great rapidity and the creeping root growth was very great. This is in accordance with Sinclair's statement that he found the creeping roots "five feet in length, the growth of a few months only". An attempt was made to get rid of this grass on the affected plots by the method recommended by Sowerby & Johnson(8) namely to go over the field digging out and then collecting with a fork, but with little effect. On the other hand, the two years' fallow in 1933 and 1934, with the succession of cultivations shown on pp. 96-7, seems to have almost got rid of this grass on the affected plots. A few pieces must have survived, for in the third year after the fallow, when continuous wheat growing has been resumed, a little *Holcus* is again (1938) prominent on the more acid plots.

Along with the above, there is always a certain amount of *Agrostis stolonifera*, but the range of this grass over the plots is far wider and it is found almost equally among the continuous wheat and barley plots. It was also found in abundance in the most acid plots (2a and 5a) both in the wheat and barley areas. On 6 February 1933, on plot 2a in the permanent barley, 23 kg. of soil, taken to 6 in. deep from all over the plot, gave 0.9 g. of *Agrostis* roots and 0.4 g. of *Holcus* roots. This is equal to 0.004 and 0.002% respectively of the whole weight of the soil, a figure which shows the way in which these grasses had taken possession of the ground in the more acid plots.

The *Agrostis* is, however, far more generally distributed over the plots and over the farm outside the plots in question than is *Holcus mollis*. It seems almost independent of the reaction of the soil, though it was noticed to be present in smaller amount on plots 6 (nitrate of soda and mineral manures, with pH value of 5.8) and 11b (farmyard manure, with pH value of 5.8).

On the whole, the fallow, done carefully as described previously in 1933 and 1934, was very effective in getting rid of the *Agrostis* twitch as well as the *Holcus* twitch, and there was a very small amount of either in the first crop after the two years' fallow was completed.

Rumex acetosella

It would be expected that in soil where all the plots are acid, sheep's sorrel (*R. acetosella*) would be found, and this has been the case. But while present on all plots, it took possession of the more acid plots in gradually increasing patches, and in places it almost replaced the acid-loving annual weeds (spurrey) particularly on plot 2a of the permanent barley. The extent to which it had taken possession before the fallow in 1933-4, is shown by a determination of the amount of roots of this weed in 23 kg. of soil taken from various parts of this plot to 6 in. deep. The roots weighed 10.1 g. or 0.044 % of the whole weight of the soil.

An attempt was made previous to the fallow to eradicate this weed on the acid plots by digging out and removing, but it was very ineffective, and the fallow itself was not nearly so useful in getting rid of it as in the case of the twitches referred to above. In the year after the fallow was completed and barley had been grown once again it was noted that on 16 September 1936, *R. acetosella* was found in nearly all the plots, while in plots 2a and 5a it was very abundant. On plot 2a it was noted that the plot was, even then, being completely invaded by *Rumex*, while it was abundant in the other extremely acid plot (5a). In fact, apart from changing the character of the soil by very heavy liming or the very large application of cattle manure, we have not found any method of clearing the land of this most pernicious weed.

Equisetum arvense

Horsetail is very common in the greensand area on which the present experiments were conducted. It is curious that this should be so, as the land is very well drained, having a subsoil of almost pure sand. The methods which are recommended to get rid of the weed by Long(6) are "draining, liming, deep cultivation, improvement of the texture of the soil by manuring, regular and persistent cutting of the . . . stems", etc. In the present case, the land is already very well drained, and the relative prevalence of the weed on the various plots will indicate how far the above recommendations are likely to be effective in getting rid of the weed.

With regard to drainage, there seems to be prevalent belief that the presence of *Equisetum* indicates poor drainage (*vide* Brenchley(3)) but the local experience at Woburn does not seem to support this idea. In fact, the weed occurs, on these greensand soils, perhaps to the greatest extent in the most completely drained and light soils, with a completely sandy subsoil.

Its distribution on the plots we are now considering is illustrated by notes on its prevalence in July 1934 nearly at the beginning of the first year's fallow. These were as follows:

Plot	
1	(Unmanured, pH 5.4.) <i>Equisetum</i> is abundant, but much less than on plot 4 (see below).
2a	(Sulphate of ammonia only, pH 4.4.) Only a few plants of <i>Equisetum</i> .
2b	(Sulphate of ammonia, with lime, pH 5.8.) More <i>Equisetum</i> than on plot 2a, but not really thick with it.
3a/b	(Nitrate of soda only, pH 5.6.) Much <i>Equisetum</i> all over the plots.
4a	(Mineral manures only, pH 5.4.) <i>Equisetum</i> all over the plot.
4b	(Mineral manures and lime, pH 5.7.) <i>Equisetum</i> all over the plot, and more than on plot 4a.
5a	(Mineral manures and sulphate of ammonia, pH 4.7.) Some <i>Equisetum</i> , but not thick with it.
5b	(Mineral manures, sulphate of ammonia, and lime, pH 5.9.) Horsetail is very thick on this plot.
6	(Mineral manures and nitrate of soda, pH 5.8.) <i>Equisetum</i> is thick all over this plot.
11b	(Farmyard manure, pH 5.8.) Much <i>Equisetum</i> .

It will be seen from this that it is only on the very acid plots that the amount of *Equisetum* is much reduced. It is, on the whole, much heavier on the plots with mineral manures than on those which, for many years, have not had such manures, while there is little difference between those which have been manured with organic manures like farmyard manure and those which have been fertilized entirely by artificial.

The fallow seemed to have less effect on the *Equisetum* than it had on any of the other perennial weeds. In the middle of the second year of the fallow (26 June 1935), notes were made of these perennial weeds with the following results.

Plot	
1	Much horsetail. No other perennials.
2a	No <i>Equisetum</i> .
2b	Few <i>Equisetum</i> plants. No other perennials.
3a/b	<i>Equisetum</i> abundant.
4a, b	Much <i>Equisetum</i> . No other perennials.
5a	No <i>Equisetum</i> .
5b	<i>Equisetum</i> abundant.
6, 11b	Not noted.

In spite of this, it may be said that since the two years' fallow was completed, we have had little trouble with *Equisetum*, though it has certainly not been eradicated, and two years after the fallow, there are still signs of the weed in many of the plots.

In connexion with this weed, I may as well record experiences in connexion with the examination of the root system of *Equisetum* on a very similar green-sand soil about a mile away from the above experimental field, where it had become a very serious pest. The whole of the soil down to 56 in. was examined. At this time the character of the soil and subsoil was as follows:

- A. 8 in. surface soil (10.3 % water).
- B. 8 in. subsoil, consisting of sand, but damp (9.1 % water).
- C. 21 in. dry layer of sand (2.4 % water).
- D. 8 in. sand, becoming more damp (3.4 % water).
- E. 8 in. damp sand, but no sign of subsoil water layer (4.6 % water).

Equisetum roots were brown bands with few short side-roots till they reach the layer of dry sand, say about 18 in. deep. There they spread horizontally and there were many side shoots. From these, thickish branches went straight downward through the remainder of the dry layer, with nut swellings at intervals. From these nuts, large finer roots went down with few side roots, but with numerous fine rootlets when they reach a moister layer. The thick roots with the nut swellings also penetrated the moister layers, but sometimes suddenly stopped. The nuts, however, sent off finer roots with many finer rootlets going to a lower depth. The greatest depth found was 5 ft. from the surface, being a continuation of a thin narrowly branched root. The nuts on the roots were found to a depth of at least 37 in.

Tussilago farfara

Before the fallow of 1934-5, there were large patches of coltsfoot on both the permanent wheat and barley land. These were all over the area and had no relationship whatever to the previous treatment, except that there were no patches in the portions where mineral manures had not been given during a period of fifty years. The thorough cultivation during the fallowing years completely got rid of this weed and, so far (1938) no coltsfoot has since been seen on any of the plots again.

Convolvulus arvensis

This very serious and injurious weed occurs, as would be expected, over almost all the type of land we are considering, but its distribution before the fallow in 1934-5 was of some interest. At this time, there was no *Convolvulus arvensis* at all in the area which had not been treated with mineral manures, i.e. on plots 1, 2 and 3. On the other hand, it occurred abundantly on plots 4 (mineral manures only, with or without lime), 5a (mineral manures and sulphate of ammonia), and 5b (the same with lime). On plot 6 (mineral manures and nitrate of soda) there was plenty of bindweed, but, curiously enough, it was not noticed on plot 11b (farmyard manure).

The experience since the two years' fallow seems to indicate that the fallow has done little to eradicate this weed, and it now prevails to almost the same extent and on the same plots as it did before the fallow was taken.

SUMMARY

1. The weed herbage has been studied in the field on a light sandy loam of slightly acid character which has been under continuous wheat and barley cropping for over fifty years, with various manurial treatments up to 1926 and with no manures since that date. A fallow was taken in 1934 and 1935 and this enabled the general character of the weed herbage to be determined, as well as the effect of fallowing and of the previous manurial treatment on each of the important weeds.

2. Analyses of the figures obtained show that in the field, with most of the important annual weeds on this soil, roughly half the year's growth of plants have germinated before the end of April. This does not, however, apply to individual weeds for the dominant one, *Spergula arvensis*, germinates regularly throughout the year, while the germination of the following weeds is very seasonal, *Polygonum aviculare* (March to May), *Gnaphalium uliginosum* (June to September), *Chenopodium album* (May and June).

3. A single year's fallow, even when accompanied by frequent cultivations at intervals of about two months except in winter, is not very effective in getting rid of the weeds which will grow on this land. Two years' fallow brings about, however, a fairly large reduction except with *Stellaria media* and *Poa annua*, neither of which appeared to be appreciably altered in amount.

4. Acidity of the soil induced by previous manuring with sulphate of ammonia had a very great influence on the weed herbage, and when the pH value was lower than 5.0 the annual plants consisted almost entirely of *Spergula arvensis*, with a small amount of *Polygonum aviculare* and *Poa annua*. *Matricaria inodora*, though an acid-loving weed, disappeared almost entirely when the pH value was less than 5.4, but was also reduced in amount when it was greater than 5.8. Each of the weeds studied seems to have a very definite range of pH value in which it is at its best. But *Polygonum aviculare* and *Poa annua* are by far the least sensitive to change in acidity of all that were found on these plots.

5. The effect of the long continued addition of mineral manures (superphosphate and muriate of potash) has been very small on the number of plants per unit area of any of the annual weeds studied, except in the case of *Vicia hirsuta* which appeared as a serious weed only in the plots which had received mineral manures or farmyard manure, and then only when the pH value was over 5.6. The annual addition of farmyard manure for fifty years has left a legacy of an increased amount of most of the weeds.

6. The effect of lime on the weed herbage is almost entirely governed by the change in acidity thereby induced. The lime does not appear to have a specific effect in any of the weeds examined.

7. The perennial weeds which tended to take possession of these plots were (a) *Holcus mollis* and *Agrostis stolonifera*, which became very serious "twiches"

in the more acid plots, but which were almost eradicated by the two years' fallow, (b) *Rumex acetosella* which also infested the more acid plots, but could not be removed by a fallow even of two years, (c) *Equisetum arvense* which seemed rather to be encouraged by the fallowing of the land, but was absent from the more acid plots. *Tussilago farfara* appeared to be indifferent to the previous treatment of the land, but entirely disappeared after the fallowing operation. *Convolvulus arvensis* did not occur on plots which had received no mineral manures in the previous half century, but its amount was hardly affected by the two years' fallow.

REFERENCES

- (1) **Batchelor, T.** *General View of the Agriculture of the County of Bedford*, p. 323, London, 1808.
- (2) **Brenchley, W. E.** "The weeds of arable land in relation to the soils on which they grow." *Ann. Bot., Lond.*, **25**, 155, 1911, and **26**, 95, 1912.
- (3) **Brenchley, W. E.** *Weeds of Farm Land*, p. 107, London, 1920.
- (4) **Brenchley, W. E. & Warington, K.** "The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations of their natural dormancy." *This JOURN.* **18**, 235, 1930. "II. Influence of crop, soil, and methods of cultivation upon the relative abundance of viable seeds." *This JOURN.* **21**, 103, 1933.
- (5) **Crowther, E. M.** *Fifty Years of Field Experiments at the Woburn Experimental Station*, by E. J. Russell and J. A. Voelcker. Part IV, by E. M. Crowther. London, 1936.
- (6) **Long, H. C.** *Weeds of Arable Land*, p. 133, London, 1929.
- (7) **Sinclair, G.** *Hortus Gramineus Woburnensis*, London, 1824.
- (8) **Sowerby & Johnson.** *Grasses of Great Britain*, London, 1861.

SEASONAL VARIATIONS IN THE ACIDITY OF SOME WOODLAND SOILS

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(With four Figures in the Text)

DETERMINATIONS made at different times of the year on soils from Bagley Wood, near Oxford, gave some evidence of a seasonal variation in acidity. In order to investigate this more fully, observations were made in chosen stations at monthly intervals through five complete years (Dec. 1932 to Nov. 1937).

DESCRIPTION OF SITES

Bagley Wood is exceptional in having a considerable variety of soil types in a comparatively restricted area. The nature of the soils and the associated vegetation at the selected stations are set out in Table I. It will be seen that the soils fall into three main groups of gravels, loams and clays, the soils within a group being derived from the same geological substratum and having similar profiles. The clays and loams were typical "mull" soils, while the gravels showed some tendency to an accumulation of raw humus and could be regarded as intermediate between the "mull" and "mor" types. G 1 and G 2 had numerous mouse runs and only a slight accumulation of raw humus, but in G 3, the most acid of the three, there was little evidence of burrowing animals and up to 3 in. of raw humus. None of the gravels showed a definite podsol profile.

Samples were taken from the uppermost and lowest layers of the profile in each soil type, as indicated in Table I. These are termed "upper layers" and "lower layers" respectively throughout this paper. The "lower layers" were sampled at 10-12 in. below the soil surface.

METHOD

The sites were marked with permanent stakes and care was taken to collect each monthly sample from a freshly cut hole. The soils were carried at once to the Laboratory and shaken in hard glass tubes with twice their volume of conductivity water which was obtained by condensation against pure tin in a still of special design. After careful comparative trials, chemically pure barium sulphate, as recommended by Kühn (1929), was added to the soil before shaking, and was found to facilitate clearing very greatly.

Table I

Soil	Geological substratum	Vegetation			Profile
		Trees	Saplings and shrubs	Ground flora	
G 1	Plateau	<i>Quercus</i> ,	—	<i>Pteridium</i> , <i>Rubus</i> , <i>Holcus</i> ,	1-3 in. litter
G 2	Gravel	<i>Betula</i>	<i>Acer Pseud.</i> (coppiced)	<i>Anemone</i> , <i>Teucrium</i>	0.5-3 in. dark brown laminated raw humus*
		<i>Betula</i>		<i>Pteridium</i> , <i>Rubus</i> , <i>Scilla</i>	
G 3		<i>Quercus</i> ,	—	<i>Pteridium</i> , <i>Anemone</i> , <i>Holcus</i> ,	4-5 in. humus-stained sand with bleached grains
		<i>Betula</i> (cleared Mar. 1935)		<i>Gal. saxatile</i> , <i>Teucrium</i> , <i>Polyt. formosum</i>	Subsoil yellow gravelly sand*
L 1	Kimmeridge Sand	<i>Quercus</i> ,	<i>Cornus</i>	<i>Pteridium</i> , <i>Rubus</i> , <i>Viola</i> ,	0-1 in. litter
L 2		<i>Fraxinus</i>	—	<i>Sanicula</i> , <i>Oxalis</i> ,	4-7 in. humus-stained sandy clay*
		<i>Fraxinus</i> ,		<i>Circaea</i>	Subsoil yellow sandy clay*
		<i>Betula</i> , <i>Acer Pseud.</i>		<i>Rubus</i> , <i>Pteridium</i> , <i>Sanicula</i> , <i>Mercurialis</i> , <i>Viola</i> , <i>Circaea</i>	
C 1	Kimmeridge Clay	<i>Quercus</i> ,	<i>Populus trem.</i> ,	<i>Rubus</i> , <i>Pteridium</i> , <i>Juncus</i> eff., <i>Carex sylv.</i>	0-0.5 in. litter
C 2		<i>Betula</i>	<i>Ligustrum</i>	<i>Rubus</i> , <i>Pteridium</i> , <i>Sanicula</i> , <i>Circaea</i> , <i>Viola</i> , <i>Teucrium</i>	6-9 in. humus-stained clay-loam*
		<i>Quercus</i> , <i>Betula</i> , <i>Acer Pseud.</i>	<i>Fraxinus</i>		Subsoil streaky blue clay with pebbles*

* Layers sampled for acidity determinations.

The soils were collected in the afternoon of one day, shaken with water as described above, and allowed to stand till the following morning, when a clear extract was obtained by centrifuging. This was tested colorometrically, using the standard solutions and indicators of Clark (1922). The primary data are tabled in the Appendix.

The soils remained in contact with water for 18-20 hr. before the clear extract was tested. Previous trials showed very slight falls in acidity during the first few hours of soaking, and only negligible changes thereafter. Table II shows the result of one such trial on a loam derived from the Kimmeridge Sand.

Table II

Depth in.	Hours soaked before testing									
	2	4	6	8	12	14	16	18	24	36
1	5.1	5.2	5.2	5.2	5.3	5.2	5.2	5.3	5.3	5.3
2	5.4	5.5	5.5	5.5	5.4	5.3	5.5	5.5	5.5	5.3
6	5.5	5.5	5.6	5.5	5.5	5.6	5.6	5.6	5.6	5.6

ESTIMATES OF ERROR

Estimates of the standard error of a single acidity determination were found in two ways: by taking one complete set of samples in duplicate, thus providing eighteen pairs of comparable determinations; and from the analysis of variance of the results for gravels, loams and clays separately. The estimate from the eighteen pairs was 0.26 and those from the Analyses of Variance were 0.24 for gravels and 0.23 for loams and clays. These estimates agree

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closely, justifying the use of high order interactions as the basis for estimating error.

Most of the comparisons made are between averages of many observations, and the standard errors are correspondingly reduced. In all tables and diagrams the appropriate "significant difference", i.e. a difference to be regarded as real on the basis of 19 to 1 odds, is always stated, or is shown as a vertical line beside the actual curves.

ANALYSIS OF RESULTS

A preliminary inspection of the results showed that the three gravels resembled each other very closely in their behaviour, as did the two loams and the two clays. It was therefore decided to present the results in the form of tables and diagrams of average values for each soil type, but to draw attention to any differential behaviour of soils of the same type. In the same way values of acidity averaged for upper and lower layers of the soil are given when there is no detectable difference in their behaviour. In the first instance analyses of variance (Fisher, 1932) were performed on the three sets of data and the results are shown in Tables III-V. Results are deemed significant when the odds in favour of their being real are at least 19 to 1. Such results are in heavy type. The items entered as $S \times D$, $M \times Y$, etc., are the "first order interactions" of soil with depth, month with year, etc.; and a significant result implies that the odds are at least 19 to 1 in favour of the statement that the two or three soils of the group in question differ in their change of acidity with depth, or that the average acidity for the soil group shows a different month to month behaviour in different years, etc.

(1) *Relation of acidity to soil type*

The average acidities over the whole period were:

Gravels	Loams	Clays
G 1 4.59	L 1 5.54	C 1 5.83
G 2 4.78	L 2 6.01	C 2 5.74
G 3 3.96		
Mean 4.44	Mean 5.77	Mean 5.78

It will be seen from the analyses of variance that in all three soil groups there are significant differences between the average acidities of the individual soils included in these groups.

(2) *Change of acidity with depth*

Considering averages over the whole period, it will be seen that the clay soils show the usual leaching gradient; the gravels show little difference between the raw humus layer and a layer 1 ft. below the surface; while the loams show a reversal of the usual gradient, the explanation of which is not clear.

Gravels	Loams	Clays
Upper layer 4.43	Upper layer 5.87	Upper layer 5.58
Lower layer 4.45	Lower layer 5.68	Lower layer 6.00

ANALYSES OF VARIANCE

Table III. *Gravels*

	Degrees of freedom	Sum of squares	Mean square	Z	Standard error
Soils	2	44.7685	22.3843	2.9981	
Depths	1	0.0302	0.0302	-0.3060	
Months	11	1.8202	0.1655	0.5444	
Years	4	22.9291	5.7327	2.3169	
S × D	2	2.1914	1.0957	1.4896	
S × M	22	0.9629	0.0438	-0.1202	
S × Y	8	4.3829	0.5479	1.1431	
D × M	11	0.4815	0.0438	-0.1202	
D × Y	4	0.6341	0.1585	0.5229	
M × Y	44	13.2066	0.3002	0.8423	
Error	250	13.9352	0.0557	—	0.2361
Total	359	105.3426	—	—	

Table IV. *Loams*

	Degrees of freedom	Sum of squares	Mean square	Z	Standard error
Soils	1	13.2071	13.2071	2.7517	
Depths	1	2.1851	2.1851	1.8521	
Months	11	0.6865	0.0624	0.0743	
Years	4	4.2831	1.0708	1.4954	
S × D	1	2.5420	2.5420	1.9277	
S × M	11	0.2464	0.0224	-0.4381	
S × Y	4	1.1269	0.2817	0.8278	
D × M	11	0.5304	0.0482	-0.0555	
D × Y	4	0.7081	0.1770	0.5955	
M × Y	44	3.5129	0.0798	0.1971	
Error	147	7.9065	0.0538	—	0.2319
Total	239	36.9350	—	—	

Table V. *Clays*

	Degrees of freedom	Sum of squares	Mean square	Z	Standard error
Soils	1	0.4951	0.4951	1.1033	
Depths	1	10.2921	10.2921	2.6205	
Months	11	1.4265	0.1297	0.4336	
Years	4	8.0174	2.0044	1.8026	
S × D	1	0.8283	0.8283	1.3606	
S × M	11	1.2544	0.1140	0.3690	
S × Y	4	1.8009	0.4502	1.0557	
D × M	11	0.6914	0.0629	0.0716	
D × Y	4	0.8631	0.2158	0.6881	
M × Y	44	4.3266	0.0983	0.2951	
Error	147	8.0172	0.0545	—	0.2335
Total	239	38.0130	—	—	

The significant S × D interaction for all types implies that the change of acidity with depth is somewhat different in the individual soils within each of the three groups.

(3) *Annual variation in acidity*

Fig. 1 shows that there is a real annual variation of acidity in all three soil types, but that the curves for gravels differ strongly from those for clays and loams. The gravels show high acidity during the first two years and much

lower acidity during the rest of the time. The clays and loams, on the other hand, show acidity falling to a minimum in 1934 and 1935, with a subsequent rise in 1936 and 1937. Both the annual variation in acidity and the different behaviour of the soil types must be explicable in terms of differences in the weather of the five seasons, since there was no other environmental factor showing marked annual variation.

Fig. 1 shows also the rainfall for the years 1933 to 1937, and the average annual rainfall in Oxford over 121 years. It is clear that the first two years of the observations were exceptionally dry, with deficits of about 6.5 and 10 in. respectively below the average. The next year, 1935, was 5.5 in. wetter than the average, and the last two, 1936 and 1937, were very close to the average.

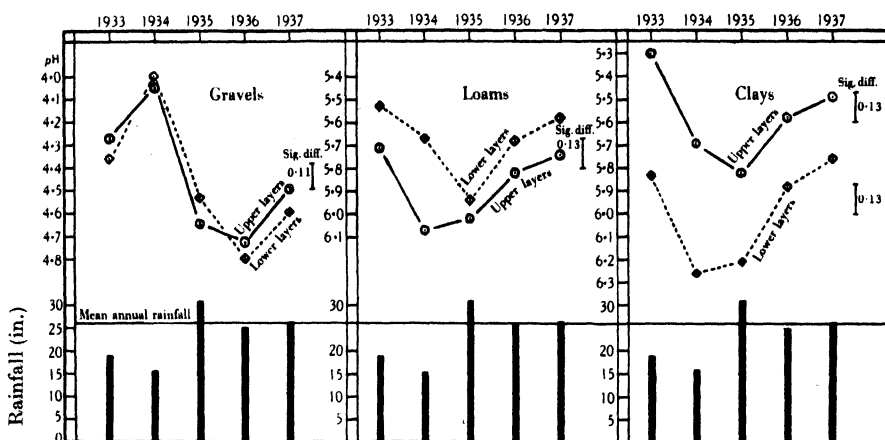


FIG. 1. Mean annual pH for the upper and lower layers of the three soil types, and total annual rainfall 1933-7.

In the interpretation of these curves increased acidity is most plausibly to be related to increased micro-organic activity. It may be suggested that the dry seasons favoured the activity of the soil population in the gravel soils, with a resulting rise in acidity. Examination of the curve (Fig. 2) showing actual monthly averages through the whole period reveals that the acidity rose during 1933 and was maintained near its highest value throughout most of the still drier season 1934. This suggests that the microflora was benefited through increased aeration by the dryness of 1933, but that the 10 in. deficit in 1934 reduced the water content of the soils below the optimal for its activity, so that there was no further increase in acidity. It is possible, too, that the high acidities developed during 1933 were themselves responsible for a reduced activity in 1934, but the most acid of the three gravels, G 3, does not show a more pronounced check than the less acid G 1 and G 2.

The higher than average rainfall of 1935 coincided with a steep fall in acidity in raw humus and in lower layers alike. There were presumably two

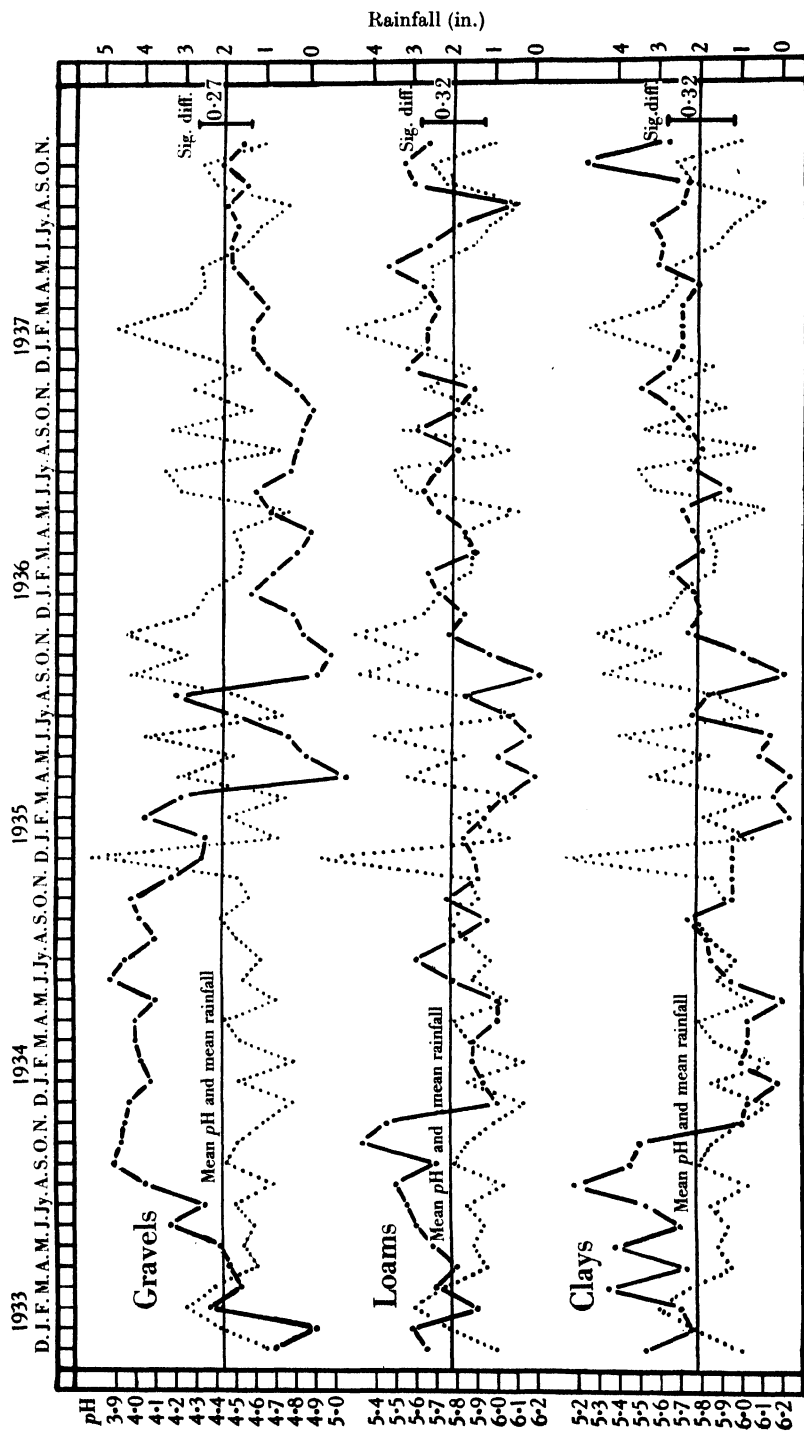


FIG. 2. Mean monthly pH (heavy lines) and monthly rainfall (dotted lines).]

factors at work here. First, accumulated acids were removed during the periods of exceptionally high rainfall; and secondly, the reduction of aeration through filling of the pore space of the soil above the optimal 50% (Waksman, 1931, p. 546), led to a reduced micro-organic activity and a consequent reduction in the rate of production of acids. The washing down of acids is suggested by the greater acidity of the lower layers than of the raw humus during much of 1935 and subsequently. The mean acidity for 1936, a year of average rainfall, shows a further significant fall which may represent a lag in recovery of the micro-organic population after the wet season of 1935. In 1937 there is a rise, presumably approaching values to be expected after a number of average seasons.

The curves of annual variation for clay soils evidently demand a different interpretation. The most obvious feature is the fall in average acidity during the dry period with a subsequent rise after wetter seasons. The explanation of this must be that ascending capillary water of high base content enriches first the lower and later the upper layers of the soil, so reducing their acidity in a dry period (Robinson, 1937). The difference in behaviour of the upper and lower layers supports this view. Since the last two years, 1936 and 1937, were of average rainfall, it is reasonable to infer that the values for 1937 approach expectations for a series of average years. This being so, the initial value for upper layers must be higher than this average, while that for lower layers must be lower (Fig. 3). In the first dry season, therefore, the upper layers showed an increased micro-organic activity, but the influence of ascending capillary water is already detectable in lower layers of the soil. It continues in both layers throughout the still drier season 1934. The upper layers, more seriously affected by the droughts, show a lag in the resumption of micro-organic activity as compared with the lower layers, and their acidity falls further in the wet year 1935, while in the lower layers there is a small rise. Through the average years, 1936 and 1937, both layers show rising acidity, presumably approaching their "normal" values.

The loams behave similarly to the clays except that here the lower layers show a continued fall in acidity during the wet season 1935, while the upper layers show a slight rise. These differences are statistically significant but they have not yet been interpreted.

(4) *Monthly variation in acidity*

Examination of Fig. 2 reveals considerable real variations in acidity from month to month, over and above the broader variations which have been related to differences in annual rainfall. These variations are specially conspicuous in the gravels in 1935, when they show a clear relation to exceptionally large variations in monthly rainfall. The steep rises in acidity in February and August of that year follow the very dry months of January and July respectively; and the low values in March to May and September to November

follow very wet periods. Similarly the high acidities in May and June of 1936 follow a dry May in that year, and, in general, periods of above-average rainfall are associated with below-average acidity and vice versa. There is some indication, therefore, of monthly variations which are related to rainfall in the same way as are the annual variations and which may be explained in the

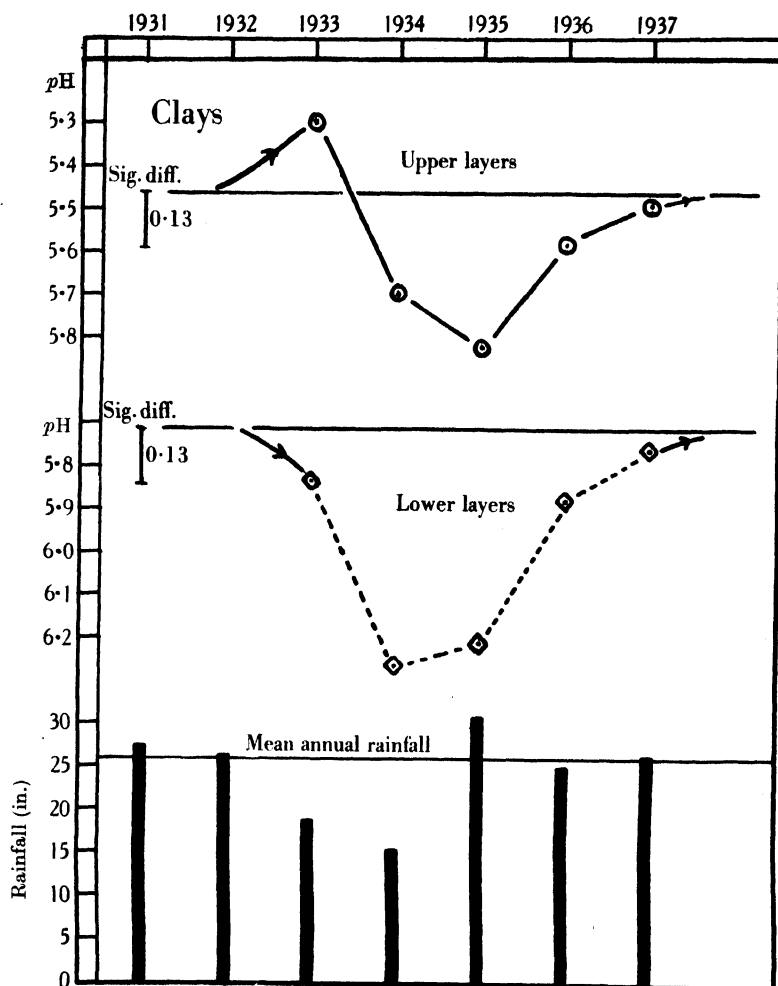


FIG. 3.

same terms—that micro-organic activity is increased in a dry period and reduced in a wet period, when acidity is further lowered by a washing down of organic acids.

With clays the relations are more obscure, the monthly variations being smaller and their errors larger. The low acidities from February to June of 1935 following the low rainfalls of January to March may perhaps be explained

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in the same way as those of the first half of 1934—the result of the capillary ascent of water rich in bases at a time when the soil is very dry to a considerable depth.

There remains a suggestion of two annual maxima of acidity in gravels, in January to February and in late summer; and of a single maximum in the clays in late summer or autumn. These annual rhythms, exaggerated in the case of gravels by the strong fluctuations of 1935, are shown in Fig. 4 which

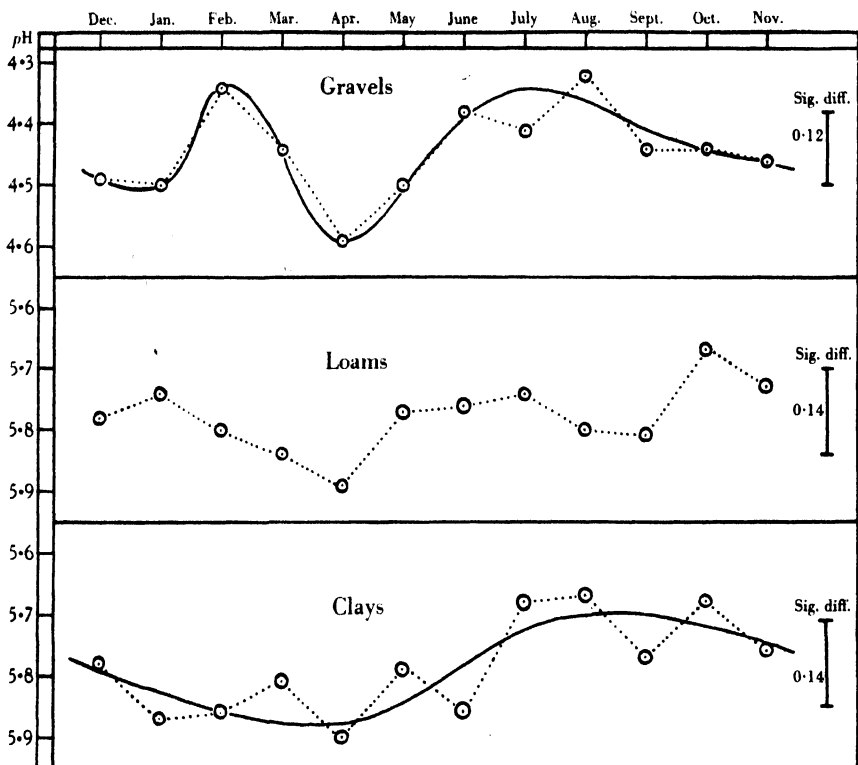


FIG. 4. Mean monthly pH: averages for the 5-year period 1933-7.

show monthly means of acidity averaged over the five years of the observations. It seems legitimate to accept these as real underlying rhythms and to explain them in terms of the well-known observation that “the numbers and activities of micro-organisms in soil change with the season of the year, due to changes in soil temperature and moisture, in production of available organic matter, soil aeration, etc. There is usually a rise in autumn and spring and a drop in winter and summer.” (Waksman, 1931). The two maxima of acidity in the gravel soils may reasonably be correlated with maxima of micro-organic activity leading to the production of organic acids. The winter depression is presumably related to low temperature and supra-optimal water content; and

the summer depression to exhaustion of substrate and drought. During periods of reduced micro-organic activity the acids are carried to lower layers, taken up by mycorrhizal fungi, etc., and the acidity of the soil is lowered.

In the clays the spring maximum can be detected only in C 2, and then not very convincingly (Table VI). It must be inferred that the colder and wetter clay soils may not provide favourable conditions for micro-organic activity until later in the season.

Table VI

	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
C 1	5.82	6.02	5.91	5.97	5.95	5.79	5.99	5.69	5.66	5.83	5.60	5.70
C 2	5.74	5.71	5.80	5.64	5.85	5.78	5.73	5.67	5.67	5.70	5.73	5.82

Significant difference 0.21.

The loams show no statistically significant annual rhythm, but there is a suggestion of a summer maximum of activity in the upper layers comparable with that in the clays.

This analysis of the monthly variations in acidity explains several of the items in Tables III-V. The significance of the item Months in gravels and clays implies that for these soil types there is a real difference between the mean values of acidity for different months, a difference which has been interpreted as due, at least in part, to a real annual rhythm in micro-organic activity. The significance of the item $S \times M$, for clays only, implies that the three gravels agree closely in the rhythm they exhibit, but that the two clays show a difference, to which reference has been made above. That the item $D \times M$ is never significant implies that in none of the soils do upper and lower layers behave differently in this respect. Finally the significance in all types of the item $M \times Y$ means that the monthly variations are not explicable entirely in terms of a constant rhythm about a mean value which varies from year to year, but that there are real variations over and above this. Some of these variations have been related to short periods of very high or very low rainfall.

It is realized that the interpretation of variations in acidity is not based on direct observation but is largely inferential. Further work, and, in particular, collaboration with soil chemists and soil microbiologists is needed before these inferences can be substantiated.

In conclusion it may be noted that these data constitute a warning against generalizations concerning month-to-month changes in soil acidity based on results collected in a single year.

SUMMARY

1. Acidity determinations have been made monthly over a period of five years on the upper and lower layers of the soil in seven stations representing three different types of woodland soil.

2. Analysis of the data shows that there are statistically significant annual and monthly variations in acidity in all three types.

3. The annual variations can be related to variations in total annual rainfall. The acidity of gravels is increased but that of clays and loams decreased during years of low rainfall.

4. The monthly variations are in part related to large monthly variations in rainfall, but there is some evidence also of an annual rhythm in acidity.

5. The acidity changes are ascribed to changes in micro-organic activity and, in the heavy soils, to the capillary ascent of base-rich water during dry periods.

This work was originally begun at the suggestion of Prof. A. G. Tansley, F.R.S., for whose interest we are very grateful. We have also had the advantage of discussing the data with Prof. W. H. Pearsall. Finally we are glad to acknowledge the assistance of Mr E. W. Arthurs in the collection and preparation of the soil samples.

REFERENCES

- Clark, W. M.** *The Determination of Hydrogen Ions*, 2nd ed. Baltimore, 1922.
Fisher, R. A. *Statistical Methods for Research Workers*, 4th ed. Edinburgh, 1932.
Kuhn, Z. *Pflanz. Düng. A*, **15**, 13, 1929.
Robinson, G. W. *Soils: Their Origin, Constitution and Classification*, 2nd ed. London, 1937.
Waksman, S. A. *Principles of Soil Microbiology*, 2nd ed. London, 1931.

APPENDIX
Primary data: pH determinations

		Upper layers												Lower layers											
		Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.
G 1	1933	4.7	4.7	4.6	4.9	4.7	4.2	3.9	4.3	4.1	4.1	3.9	4.3	5.1	5.5	4.5	4.8	4.7	4.9	4.4	4.4	4.4	3.9	3.9	3.7
	1934	4.1	4.3	4.0	3.9	3.9	4.2	3.9	3.9	4.1	4.1	4.3	4.0	4.1	4.3	4.1	4.1	4.0	4.2	3.9	4.0	4.0	4.1	4.0	4.3
	1935	4.3	4.7	4.0	4.0	5.1	5.1	4.5	4.7	3.9	5.1	4.8	4.8	4.5	4.3	4.1	4.3	5.1	4.8	5.3	4.7	4.7	4.9	5.6	4.9
	1936	4.7	4.3	4.7	4.9	5.3	4.9	4.9	4.9	4.9	5.3	4.9	4.7	5.3	5.1	5.1	5.3	5.1	4.9	4.9	5.1	5.3	5.5	5.5	5.3
	1937	4.9	4.8	4.6	4.7	4.7	4.7	4.7	4.1	4.1	3.9	4.1	4.1	5.1	5.3	5.1	5.3	4.7	4.7	4.7	4.7	4.8	5.1	5.1	5.5
	1933	4.5	4.9	4.6	4.6	4.6	4.5	4.6	4.0	4.1	4.2	4.3	4.3	4.7	5.3	4.7	4.9	4.8	5.1	4.7	4.6	4.8	4.1	4.2	4.2
	1934	4.2	4.3	4.5	4.3	4.2	4.3	4.1	4.3	4.2	4.1	4.2	4.4	4.3	4.3	4.3	4.3	4.3	4.1	4.1	4.2	4.1	4.1	4.1	4.3
G 2	1935	5.1	4.9	4.7	4.9	5.5	5.5	5.3	4.7	4.5	5.1	5.5	5.3	4.7	4.6	4.2	4.6	5.3	5.5	5.2	5.1	4.3	5.1	5.1	5.1
	1936	5.3	5.2	5.4	5.3	5.1	5.1	5.3	5.3	5.3	5.5	5.1	5.1	5.3	5.0	4.9	5.1	5.1	5.1	4.9	5.3	4.9	5.1	5.3	5.0
	1937	5.3	4.9	4.9	5.1	5.5	5.1	4.7	5.1	5.1	4.9	5.1	5.1	4.7	4.7	5.3	5.0	4.9	4.8	4.9	4.7	4.7	5.1	4.3	4.9
	1933	4.7	4.5	3.9	3.9	3.9	3.7	3.7	3.7	3.7	3.9	3.7	3.7	4.5	4.5	3.9	4.1	3.9	3.8	3.7	3.7	3.5	3.5	3.5	3.5
	1934	3.6	3.6	3.6	3.7	3.9	3.7	3.6	3.7	4.5	4.1	3.7	4.4	3.5	3.7	3.7	3.7	4.2	4.1	3.9	3.7	3.6	3.6	3.6	3.7
	1935	3.7	4.1	3.6	3.9	5.1	4.1	4.1	3.9	3.9	5.1	4.7	4.8	3.7	3.7	3.7	3.7	4.2	4.1	4.1	3.9	3.9	4.1	4.1	4.1
	1936	4.0	3.9	3.9	4.1	4.3	3.7	3.9	4.3	4.5	3.9	4.3	3.9	4.1	3.9	4.1	4.1	4.1	4.1	3.9	3.9	4.1	3.9	4.3	4.6
G 3	1937	3.8	3.7	3.7	3.9	3.9	3.7	3.9	3.9	4.1	4.2	4.3	3.9	4.1	4.1	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9	3.9
	1933	5.8	5.5	5.9	5.5	5.8	5.7	5.7	5.3	5.5	6.1	5.4	5.9	5.0	5.0	5.5	5.3	5.5	5.3	5.3	5.1	5.1	5.0	4.7	4.5
	1934	6.2	5.9	5.8	5.8	6.5	6.1	5.3	5.5	5.5	6.1	5.9	6.1	5.3	5.0	5.1	5.1	4.9	5.3	5.5	4.9	5.3	5.4	5.0	5.3
	1935	5.7	6.2	5.9	6.1	6.0	6.1	5.9	5.5	5.5	6.1	5.5	5.7	5.5	5.1	5.5	5.3	6.1	5.6	6.1	5.7	5.7	6.1	5.9	5.7
	1936	5.6	5.9	5.6	6.2	5.8	5.5	5.2	5.3	5.7	5.7	5.7	6.1	5.7	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	4.7	5.7	5.7
	1937	5.7	5.3	5.7	5.3	5.5	5.5	5.7	5.7	6.1	5.3	5.1	5.5	4.7	5.5	5.1	5.4	5.1	4.8	5.1	5.5	5.8	5.3	5.2	5.1
	1933	5.9	5.9	5.9	6.1	5.9	5.8	5.5	5.9	5.7	5.7	5.5	5.1	5.9	5.9	6.3	5.9	6.0	5.9	5.9	5.9	5.7	6.0	5.7	6.3
L 1	1934	6.3	6.5	6.3	6.3	6.3	6.2	6.1	6.1	6.1	6.2	6.2	6.1	6.2	5.9	6.1	6.3	6.3	6.2	6.1	5.9	6.2	6.1	5.9	6.1
	1935	6.1	6.1	6.2	6.4	6.3	6.2	6.1	6.3	6.0	6.3	6.1	5.5	6.2	5.9	6.1	6.3	6.2	6.2	6.3	6.3	6.1	6.3	6.3	6.1
	1936	6.0	5.7	5.9	5.7	6.1	5.9	5.9	6.1	6.1	6.1	5.9	5.9	6.0	5.7	5.6	5.7	5.9	5.9	5.9	5.9	5.9	5.9	5.9	5.8
	1937	5.9	5.9	5.9	6.0	6.1	5.7	5.9	6.1	6.1	5.8	6.1	6.1	5.9	5.9	5.9	6.1	5.8	5.8	5.9	5.9	6.3	5.9	5.9	5.9
	1933	5.8	5.5	5.9	5.5	5.8	5.7	5.7	5.3	5.5	6.1	5.4	5.9	5.0	5.0	5.5	5.3	5.5	5.3	5.3	5.1	5.1	5.0	4.7	4.5
	1934	6.2	5.9	5.8	5.8	6.5	6.1	5.3	5.5	5.5	6.1	5.9	6.1	5.3	5.0	5.1	5.1	4.9	5.3	5.5	4.9	5.3	5.4	5.0	5.3
	1935	5.7	6.2	5.9	6.1	6.1	6.0	6.1	5.9	5.5	6.1	5.5	5.7	5.5	5.1	5.5	5.3	6.1	5.6	6.1	5.7	5.7	6.1	5.9	5.7
L 2	1936	5.6	5.9	5.6	6.2	5.8	5.5	5.2	5.3	5.7	5.7	5.7	6.1	5.7	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	4.7	5.7	5.7
	1937	5.7	5.3	5.7	5.3	5.5	5.5	5.7	5.7	6.1	5.3	5.1	5.5	4.7	5.5	5.1	5.4	5.1	4.8	5.1	5.5	5.8	5.3	5.2	5.1
	1933	5.9	5.9	5.9	6.1	5.9	5.8	5.5	5.9	5.7	5.7	5.5	5.1	5.9	5.9	6.3	5.9	6.0	5.9	5.9	5.9	5.7	6.0	5.7	6.3
	1934	6.3	6.5	6.3	6.3	6.3	6.3	6.2	6.1	6.1	6.2	6.2	6.1	6.2	5.9	6.1	6.3	6.3	6.3	6.1	5.9	6.2	6.1	5.9	6.1
	1935	6.1	6.1	6.2	6.4	6.3	6.2	6.1	6.3	6.0	6.3	6.1	5.5	6.2	5.9	6.1	6.3	6.2	6.2	6.3	6.3	6.1	6.3	6.3	6.1
	1936	6.0	5.7	5.9	5.7	6.1	5.9	5.9	6.1	6.1	6.1	5.9	5.9	6.0	5.7	5.6	5.7	5.9	5.9	5.9	5.9	5.9	5.9	5.9	5.8
	1937	5.9	5.9	5.9	6.0	6.1	5.7	5.9	6.1	6.1	5.8	6.1	6.1	5.9	5.9	5.9	6.1	5.8	5.8	5.9	5.9	6.3	5.9	5.9	5.9
C 1	1933	5.3	5.7	5.3	5.3	5.5	4.8	5.3	5.1	5.0	5.3	5.6	5.7	5.7	6.3	5.9	5.8	5.8	5.9	6.5	6.1	5.6	5.8	5.5	6.1
	1934	5.7	6.2	6.1	6.1	5.9	6.1	5.9	5.9	5.7	5.8	5.8	5.8	6.7	6.7	6.5	6.7	6.7	6.5	6.3	6.1	5.8	6.1	6.3	6.3
	1935	5.7	5.7	6.1	6.1	6.1	5.9	5.1	5.5	5.1	5.5	5.5	5.7	6.3	6.6	6.6	6.7	6.4	6.1	6.5	6.3	6.1	6.3	6.5	5.9
	1936	5.3	5.5	5.5	5.7	5.5	5.3	5.9	5.3	5.7	5.5	4.9	4.9	6.2	6.1	5.7	6.1	5.9	5.9	6.2	6.0	5.9	5.9	6.1	5.9
	1937	5.3	5.5	5.5	5.3	5.8	5.5	5.3	5.3	5.1	5.5	4.7	5.1	6.0	5.9	5.9	5.9	5.9	5.7	5.9	5.7	6.0	5.1	5.1	5.6
	1933	5.5	5.5	5.3	4.6	5.7	5.1	5.3	5.0	4.7	5.2	5.2	6.1	5.6	5.5	6.3	5.7	5.9	5.7	5.7	5.9	5.4	5.5	5.7	6.1
	1934	5.4	5.5	5.1	4.8	5.2	6.1	5.3	5.5	5.7	5.6	5.6	5.5	6.3	6.3	6.3	6.5	6.3	6.1	6.1	5.9	5.9	5.5	6.1	6.2
C 2	1935	5.5	5.4	6.1	5.7	6.1	6.0	6.1	5.5	5.7	5.5	5.7	5.5	6.3	6.1	6.1	6.1	6.1	6.1	6.0	6.1	6.0	6.3	5.9	5.5
	1936	5.8	5.7	5.7	5.8	5.7	6.1	5.7	5.9	5.7	5.7	5.9	5.5	5.8	5.7	5.7	5.7	5.8	5.9	5.5	5.9	5.9	5.6	6.1	5.7
	1937	5.7	5.7	5.7	5.7	5.7	5.5	5.5	5.5	6.0	5.5	5.5	5.9	5.5	5.7	5.7	5.9	5.7	5.7	5.6	5.7	5.7	5.7	5.6	5.6
	1937	5.7	5.7	5.7	5.7	5.7	5.5	5.5	5.5	6.0	5.5	5.5	5.9	5.5	5.7	5.7	5.9	5.7	5.9	5.6	5.7	5.7	5.7	5.6	5.6

THE VEGETATION OF CAPE NAPIER, SPITSBERGEN

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SCOPE AND AIMS

THE work here described was done during the month 21 July–19 August 1936, while the party of which I was a member was centred at Bruce City, Klaas Billen Bay, a branch of Ice Fjord, West Spitsbergen, in lat. $78^{\circ} 39' \text{ N.}$, long. $16^{\circ} 45' \text{ E.}$ This district has been visited several times by Oxford University Expeditions, and descriptions of the vegetation are to be found in papers by J. Walton (1922) and Summerhayes & Elton (1928). In addition, A. M. Acock has been carrying on, during 1936 and 1937, an investigation at Bruce City of wider scope.

Arctic studies limited to a single summer visit are necessarily incomplete and likely to be of small value if they remain isolated. The aim has been in this paper to build upon foundations already laid by reinvestigating a small and readily identifiable area in the high Arctic, of which the vegetation has been described before, sufficiently long ago to allow of changes having occurred.

For this reason the work has been limited to the area lying close behind Cape Napier, which was mapped by Walton in 1921 with a view to reinvestigation by some "future observer".

The chief objects of the paper are therefore:

- (1) To record any changes which may have occurred in the intervening fifteen years,
- (2) To provide a more detailed description for the benefit of later observers.

TOPOGRAPHY

For a description of the general topography of the district readers are referred to the paper of J. Walton (1922). The Cape itself, however, may be briefly described here, with reference to the map in Fig. 1.

It is a shingle promontory, for the most part about 350 yards wide, pointing roughly north by east, at the junction between Klaas Billen Bay and Adolf Bay, and it ends a long stretch of raised shingle beach which borders the east side of Klaas Billen Bay.

Along the terminal 600 yards a strong northward shore current is undercutting the shingle, leaving a steep bank which, farther south, is now protected by a broad apposition beach. On the landward side there is a series of tidal mudflats, of which, however, only a small part is colonized by plants. Beyond

the tidal limits on the silt, summer streams formed by the melting of the snow on the Campbell Range about a mile inland have formed an area of bogs and fresh-water pools. A number of shingle laterals from the main beach form partial bars across this silted area.

The factors at work are complex, but it seems that the promontory is of the familiar type described by Oliver (1912), formed by a longshore current where the land takes an inward course.

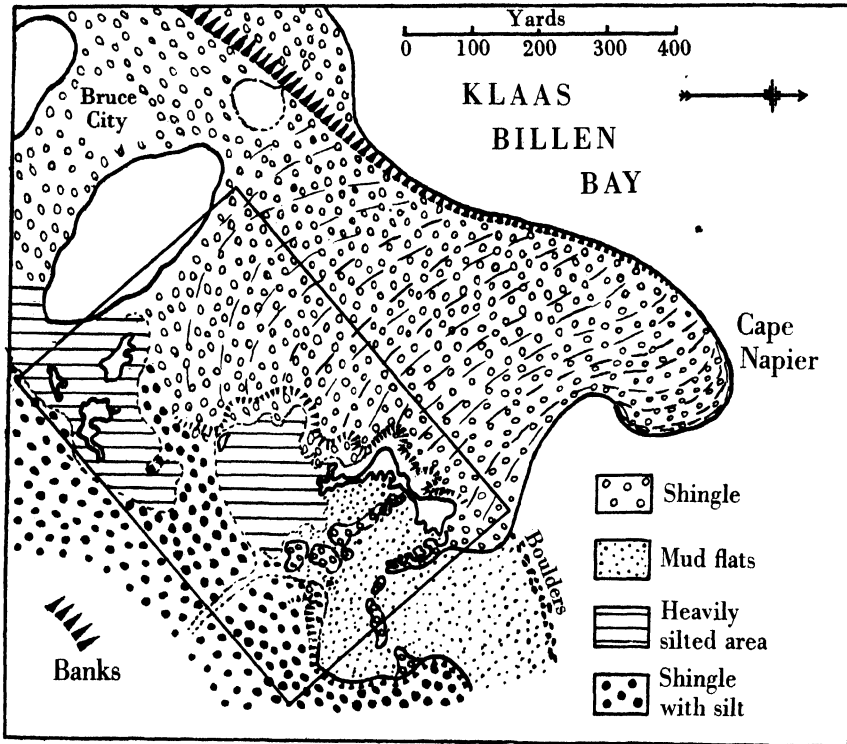


Fig. 1. Cape Napier—topographical sketch-map based upon a rough survey. The rectangle encloses the area shown in Fig. 2.

Important differences which have to be borne in mind when it is compared with British coastal spits such as Blakeney Point are: that it is in relatively sheltered inland water, frozen for a great part of the year, mobility of the shingle is reduced to a minimum by the presence of ground-ice, which is found at a depth of 30 in. or less even in midsummer, the Cape is subjected to extremely cold northerly winds from the inland ice-cap, and, while ordinary sea drift is plentiful, there is a negligible quantity of salt-marsh drift, which brings practically no plants capable of colonizing the shingle.

The main shingle beach of Cape Napier is traversed by a series of swales or "beach depressions" (see Pl. III, phot. 1), the direction of which is indicated

by the broken lines on the maps (Figs. 1, 2). The origin of these can be seen on the rounded distal part of the Cape where a series of steep ridges and furrows is in process of formation, some of the ridges becoming spits at high tide. The cause has probably been wave action combined with the action of longshore currents, piling up morainic material from the nearby Nordenskiöld Glacier on a rising beachline (see Johnson, 1919, Chap. 9). Whether the beach is still rising, however, is uncertain. Elton & Baden-Powell (1931) state: "...in the case of Klaas Billen Bay there is some evidence that this uplift has been continued until comparatively recent times."

TOPOGRAPHICAL CHANGES

The position of the area studied, in relation to its environment, is shown by Walton (1922) in Figs. 1, 2, and Pl. VI, fig. 1. It is in the innermost part of the Inner Fjord Zone, as described by Summerhays & Elton (1928).

My Fig. 2 shows a plane table survey of the same piece of land as Walton's Fig. 4, but I extended the map towards the south to include the borders of pool VI and of the inner raised beach. Walton's numbering of the pools is retained and two small pools not marked on his map, between pools V and VI, are numbered *V a* and *V b* to preserve the sequence.

Topographical changes during the fifteen years since Walton's survey have been slight. The outer shingle spit was found to have changed shape and grown in length by about 12 ft. Pool V has now disappeared altogether and is occupied by wet "tundra" vegetation with fresh "polygon-marks". On the other hand, pools *V a* and *V b* have evidently grown in size and are now definite sheets of standing water, without much vegetation in them.

However, the amount of water in the pools varies very much from year to year, as well as from season to season. Pool II, and other pools which were dry in 1936, contained water in 1937, which was evidently a wetter year.¹

METHODS

The vegetation map (Fig. 2) was sketched in on the plane table, but the mapping by eye, particularly of transition zones, was found to be unsatisfactory. Moreover, the area was too large to allow of intensive studies such as belt transects in the time available. Recourse was therefore had to ring sampling as an aid to the detailed study of the vegetation.

The method of Raunkaier (1934) of taking single samples at regular intervals along a fixed line was found unsuitable on the open communities of the shingle beach, but after some experiment a modification of it was used, which may be called the "frequency transect" method, and which has the advantage of enabling the frequencies to be plotted on a graph. Instead of isolated samples at fixed intervals, at each point on the line ten samples were taken

¹ I am indebted to Mr A. M. Acock for the 1937 observations.



Phot. 2. "Pioneers" established in depression in bare shingle. Mount Campbell in background.



Phot. 4. Pool IV taken from south-east end. Pool III in background. The dark area in foreground is the *Carex subsp. thalassia* zone.



Phot. 1. Outer shingle beach showing "beach depressions". Moisture area with *Carex* in foreground.



Phot. 3. *Dryas* "Fjaeldmark" I.

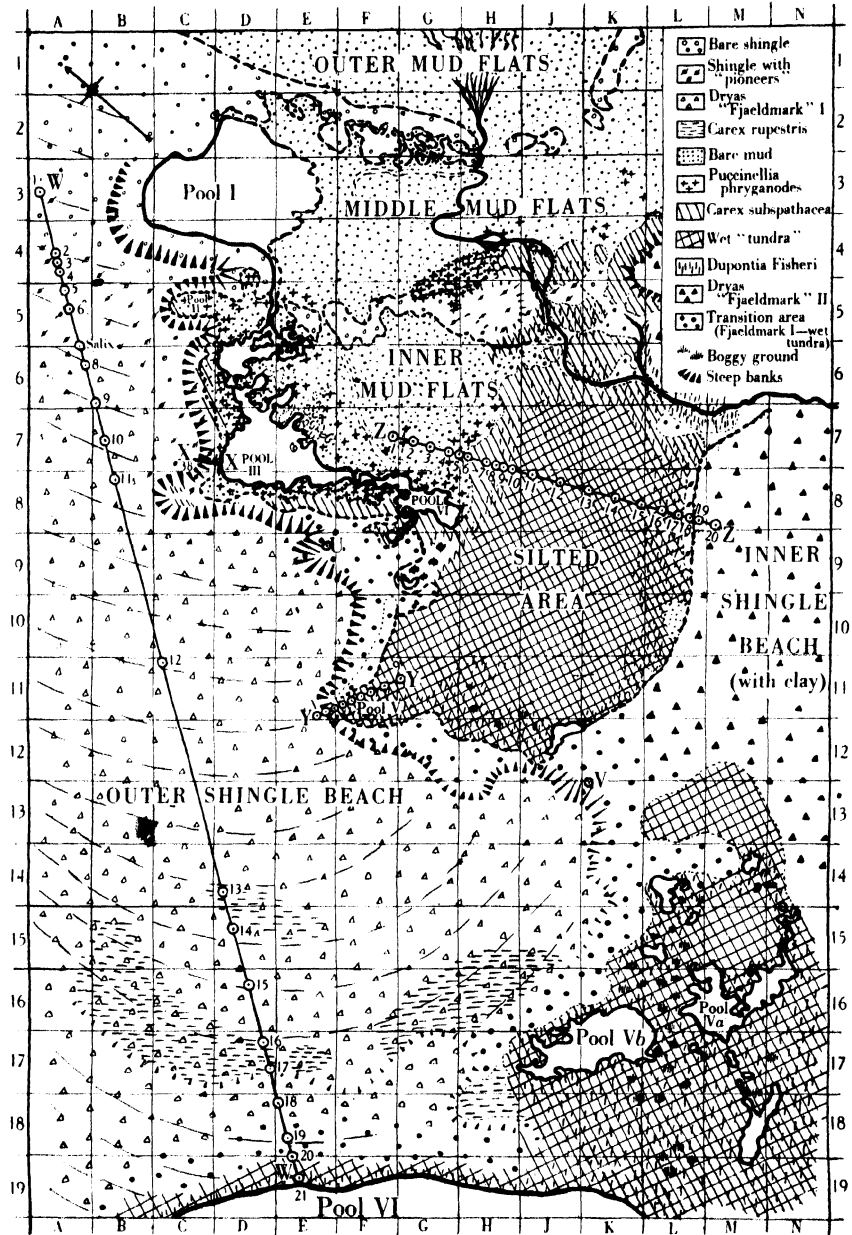


FIG. 2. Vegetation map based upon a plane-table survey covering the same ground as Walton's Fig. 4 (1922). The map is divided into 100 ft. squares which are referred to in the text with the numeral first (thus—4 G). References to the points on the frequency transects have the letter first (W 3).

W 234 56 78 9 10 11 12 13 14 15 16 17 18 19 20 21 W

Cochlearia officinalis

Cerastium alpinum

Sagina intermedia

Saxifraga oppositifolia

Saxifraga caespitosa

Mosses

Lecanora epibryon

Rhizocarpon geographicum

Cetraria nivalis and C. hirsuta

Caloplaca bracteata

Salix polaris

Dryas octopetala

Carex rupestris

Pedicularis lanata

Polygonum viviparum

Carex misandra

Saxifraga aizoides

Saxifraga hirculus

Draba alpina

Deschampsia borealis

Juncus biglumis

Carex subspathacca

Equisetum arvense var. alpestre

C. 2

Agarics

Cardamine pratensis

25
20
15
10
5
ft.

Profile of line W

ADOLPH BAY

40 0 32 42 62 82 92 112 132 152 252 377 397 427 457 472 492 512 534

Yards

POOL V

FIG. 3. Frequencies from 0 to 10 for plants along the line W (see Fig. 2), obtained from 10 throws of a 6½ in. ring within 6 ft. of each point marked on the line. The sign + indicates that the plant was seen within the area sampled, but was not included in any throw of the ring.

This method was intended to assist and clarify, rather than to supersede, ordinary observation, and where the vegetation was seen to change the interval was shortened, and, on the other hand, on the shingle beach time was saved by omitting the sampling over large areas where no change was visible.

In this way frequencies from 0 to 10 were obtained at intervals for plants occurring along the three straight lines W, Y and Z (see Fig. 2). The frequencies were plotted on composite graphs (Figs. 3, 5, 6), and with the aid of observations on the continuity of the vegetation made on the spot, the points on the graphs were joined together to give some representation of the distribution of the species along the lines chosen.

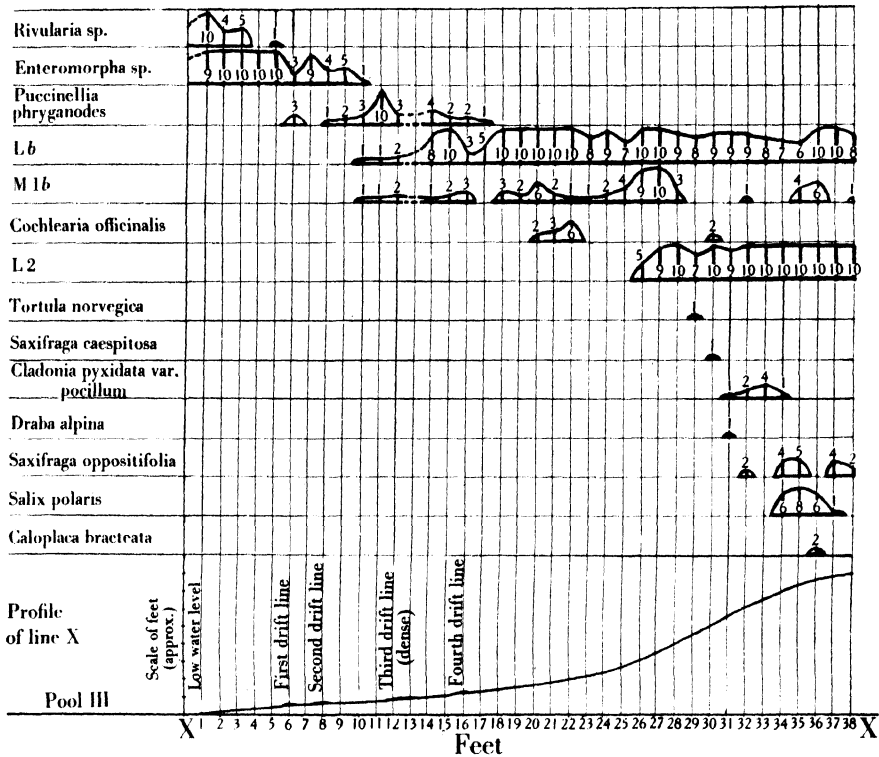


FIG. 4. Frequencies from 0 to 10 obtained by sampling with a $6\frac{1}{2}$ in. ring, divided into ten equal parts, at 1 ft. intervals along the line X (see Fig. 2).

Fig. 4, which shows the frequencies along line X, differs from the others in that it aims at greater detail. For this purpose the ring was divided into ten equal parts, and placed down at intervals of 1 ft., the frequencies recorded being the number of parts in which the species occurred.

The study of the mosses and thallophytes presented special difficulties, as it is seldom possible to identify in the field and score separately, even under arbitrary designations, the different species in a complex community, e.g. of blue-green algae or lichens. It was therefore found necessary to score only the distinguishable "complexes" under some symbol, and to attempt to identify the components later.

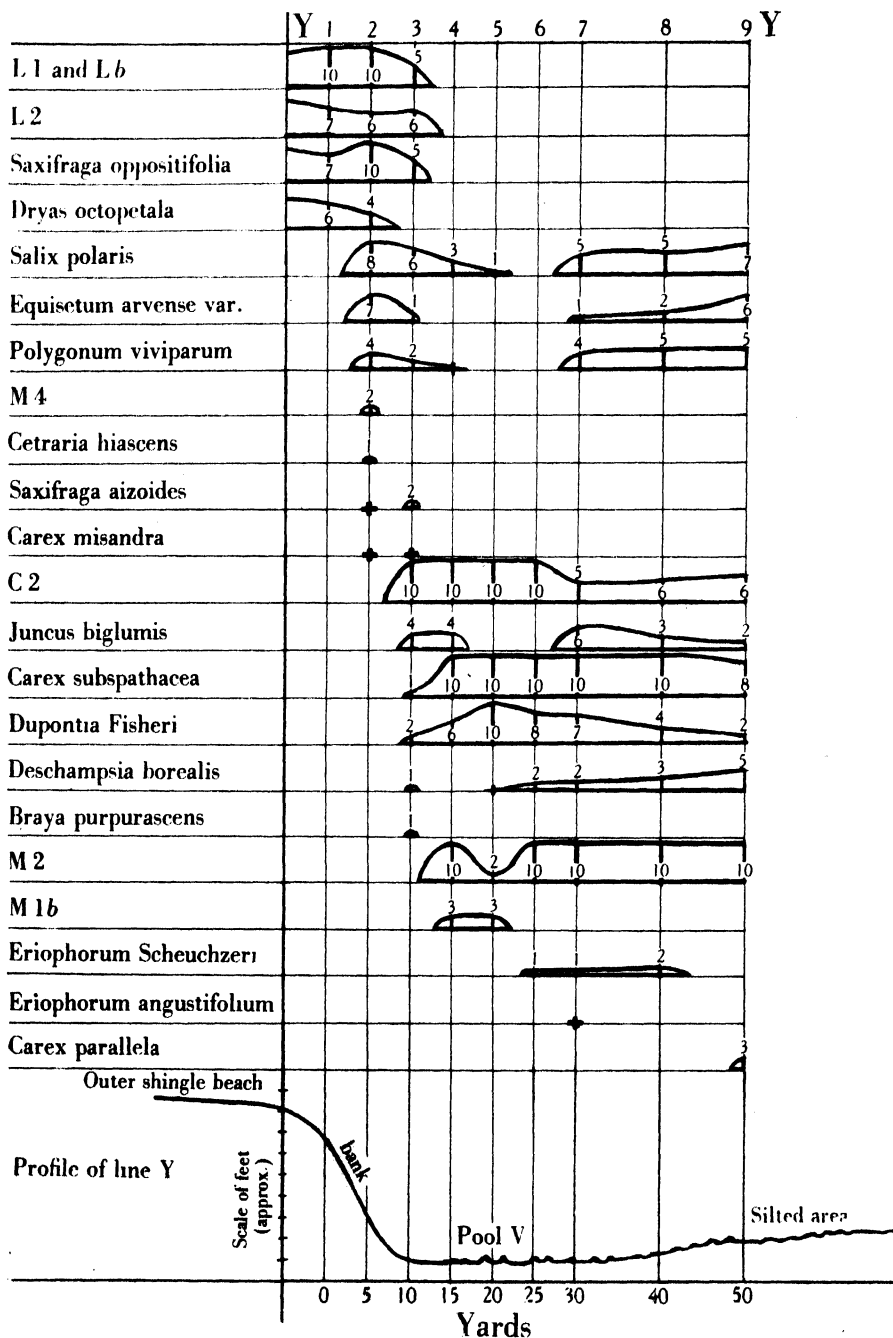


FIG. 5. Frequencies from 0 to 10 for plants along the line Y (see Fig. 2).
Particulars as for Fig. 3.

Frequently, however, the systematist is unable to identify stunted or infertile forms of lichens or mosses, although they may nevertheless contribute

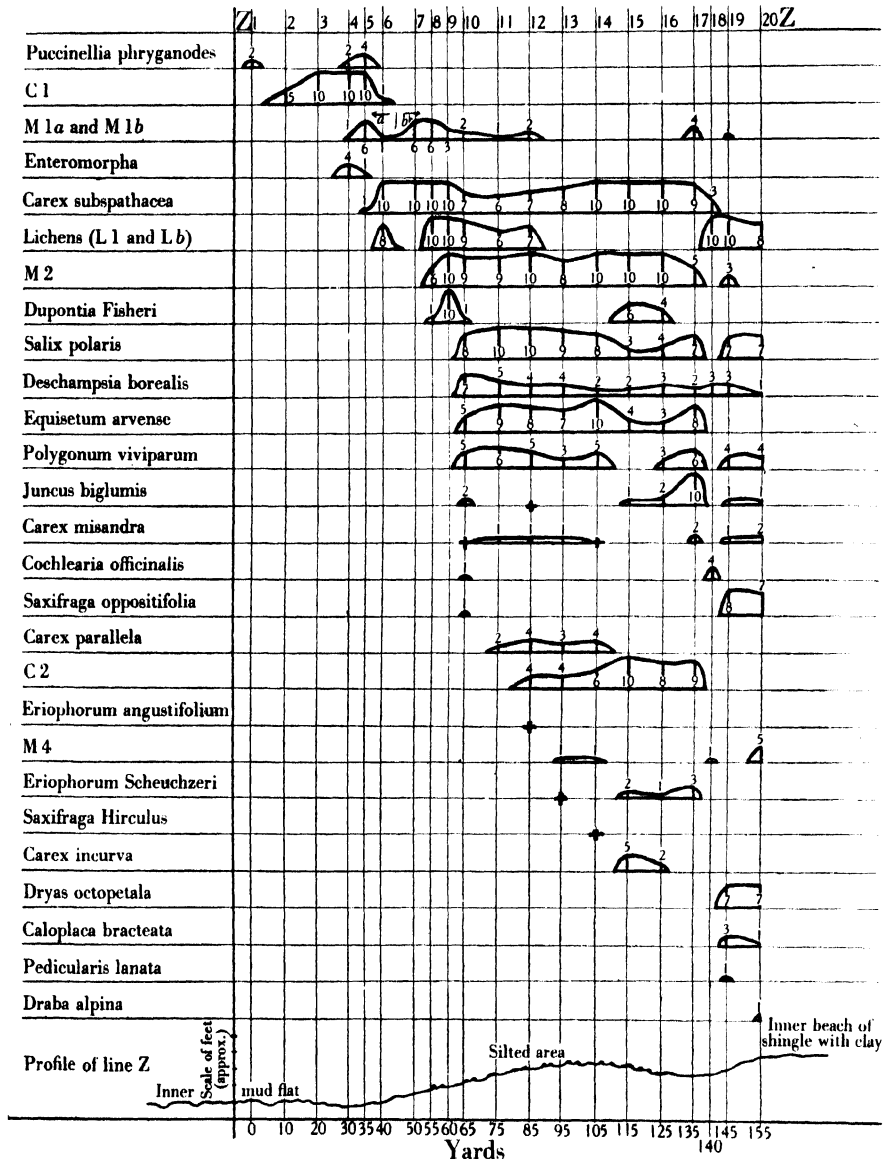


FIG. 6. Frequencies from 0 to 10 for plants along the line Z (see Fig. 2).
Particulars as for Fig. 3.

largely to the "complex", which remains, therefore, for the present the ultimate determinable unit of vegetation, and a subject for further investigation.

A list of these "complexes" is here given, with sufficient description, it is hoped, to enable other workers to identify them.

The changes in nomenclature since 1921 have been so considerable that to avoid confusion in comparing Walton's paper with this, it seems advisable also to give a list of the more important synonyms.

List of Abbreviations denoting "complexes"

Cyanophyceae:

- C 1. Wrinkly slime on surface of mudflats, chiefly *Calothrix* sp.
- C 2. Brownish sheets, chiefly *Nostoc* sp., in damper parts of wet "tundra".
- C 3. Black belt, mostly of *Rivularia* sp., on shingle bordering pool V bog, and also in small amount at edge of pool III.
- L b. See below under Lichens.

Lichens:

- L 1. Greyish white crust of imperfect stages, sterile and unidentifiable. Probably of variable constitution, but containing a large amount of *Lecanora epibryon*. Basal squamules of *Cladonia pyxidata* vars. sometimes recognizable.
- L b. A black crust consisting of L 1 covered with Cyanophyceae, chiefly *Gloeocapsa* sp.
- L 2. A complex dominated by *Lecanora epibryon* (Ach.) Ach., but often containing other sterile lichen material.

Mosses:

- M 1 a. *Swartzia inclinata* Ehr., possibly with some *S. montana* Lindb. The only critical difference between these two mosses is the oblique capsule in *S. inclinata*, which is indistinguishable in stunted specimens, such as are found on the mudflat.
- M 1 b. *Swartzia inclinata* with some recognizable *S. montana*, mixed with *Bryum nitidulum* Lindb. and occasionally *Pottia Heimii* Fuernr. Found on banks and slopes surrounding the mudflat.
- M 2. Complex of brown *Hypnum* mosses on the wet "tundra"; chiefly *Drepanocladus brevifolius* (Lindb.) Warnst., with *Orthothecium chryseum* B. & S., *Hypnum stellatum* Schreb. and *Drepanocladus vernicosus* (Lindb.) Warnst.
Camptothecium nitens (Schreb.) Schimp. and *Cratoneuron falcatum* (Brid.) Roth. were found only on the drier part of the wet "tundra", and *Drepanocladus revolvens* (Sw.) Warnst. only in the wettest part. *Aulacomnium turgidum* Schwaeg. occurs locally, probably on bird-manured sites.
- M 3. Green fringe of mosses on margin of pool VI, among which were identified: *Hypnum stellatum*, *Mnium affine* var. *elatum* Br. & Sch., *Philonotis fontana* Brid., and the rare *Calliergon giganteum* var. *cyclophyllotum* (Holz.) Grout.
- M 4. Dark brown patches of moss on shingle bank near the wet "tundra" consisting chiefly of *Barbula lurida* Lindb. and *Tortula ruralis* Ehrh.
- M 5. Isolated small patches on barer part of shingle beach near pools II and III. *Swartzia montana*, *Tortula norvegica* Wahl. and *Pleurochaete squarrosa* Lindb. (a new record for Spitsbergen) were identified from this material.
- M 6. *Bryum globosum* Lind. var. *ruberrimum* Dixon (easily recognizable by its bright red capsules) with some M 4—found on the part of the shingle beach approaching pool VI.

List of synonyms

This paper	Walton's paper (1922)
<i>Carex subspathacea</i> Wormsk.	<i>Carex salina</i> Wahlb. var. <i>subspathacea</i> Wormsk.
<i>Eriophorum angustifolium</i> Rott. f. <i>triste</i> Th.Fr.	<i>Eriophorum polystachyum</i> L. f. <i>triste</i> Th.Fr.
<i>Luzula nivalis</i> Laest.	<i>Luzula hyperborea</i> R.Br.
<i>Puccinellia phryganodes</i> (Trin.) Scribner and Merrill	<i>Glyceria vilfoidea</i> Fr.
<i>Swartzia inclinata</i> Ehr.	<i>Distichium capillaceum</i> L.

THE VEGETATION

The three main communities in the area may be called: (i) *Dryas* "Fjaeldmark", on the shingle beaches; (ii) salt marsh, on a small part of the tidal mudflats; (iii) wet "tundra", on the silted area.

(i) *Dryas* "Fjaeldmark"

It is convenient to use this term which has been used by previous authors, for the open-looking vegetation on the shingle beaches. Actually, however, there is very little true open fjaeldmark, in the sense of the term used by Warming (1909), in the area studied, except near the point of Cape Napier.

The dominant phanerogams on the outer shingle beach are *Saxifraga oppositifolia* and *Dryas octopetala*, of which the conspicuous isolated tussocks (see Pl. III, phot. 3, and Pl. IV phot. 7) give the appearance of an open community. The shingle, however, is closely covered with crustaceous or minutely foliose lichens, among which *Lecanora epibryon* (Ach.) Ach. is dominant, and *Rhizocarpon geographicum* (L.) DC., *Lecidia pantherina* (Ach.) Th.Fr., *Caloplaca bracteata* (Hoffm.) Jatta and *Cladonia pyxidata* vars. *pachythallina* and *pocillum* (Ach.) Flot. (basal squamules only) are abundant. Among the frequent and more conspicuous fruticose forms *Cetraria nivalis* Ach., *Cetraria hiascens* Th.Fr., *Stereocaulon alpinum* Laur. and *Thamnolia vermicularis* (Sw.) Ach. were identified.

Within the area studied, two varieties of this *Dryas-Saxifraga*-lichen community were found: Fjaeldmark I, on the unsilted shingle beach of Cape Napier, and Fjaeldmark II on the shingle with silt of the inner raised beach. Table I gives percentage frequencies, based on 100 ring samples, on these two beaches.

Table I

	Fjaeldmark I Outer unsilted shingle beach	Fjaeldmark II Inner shingle beach with silt
Lichens (chiefly L 1 and L 2)	100	83
<i>Saxifraga oppositifolia</i> L.	83	79
<i>Dryas octopetala</i> L.	51	71
<i>Carex rupestris</i> All.	17	0
<i>Carex misandra</i> R.Br.	9	15
Mosses (M 4 and M 5)	5	13
<i>Salix polaris</i> Wg.	3	68
<i>Pedicularis lanata</i> Willd.	2	6
<i>Polygonum viviparum</i> L.	1	38
<i>Deschampsia borealis</i> (Trautv.) Roshev.	0	23
<i>Juncus biglumis</i> L.	0	10
<i>Draba alpina</i> L.	0	4

Certain facts which were borne out by observation are illustrated by these frequencies. Of the two dominants, *Saxifraga* has a wider range of moisture tolerance than *Dryas*, since it was found on the barest shingle well in advance of *Dryas*, and also occasionally on the wet "tundra" where *Dryas* is quite absent. The frequencies recorded for the saxifrage are probably too low, since

it is easy to miss its straggling runners among the dense tussocks of *Dryas*, but it appears to flourish about as well on the unsilted as on the silted beach.

On the silted beach *Salix polaris* joins these two as a co-dominant, and the flora is enriched by the addition of *Polygonum viviparum*, *Deschampsia borealis*, and *Juncus biglumis*.

Salix is quite absent from the outer beach, except for a zone of stunted plants at 5-6 A (Fig. 2) 10 yards in advance of the first *Dryas* on the bare northerly part of the beach. The presence of *Salix* here is difficult to understand, as normally it appears to be less tolerant of drought and wind than *Dryas*, and its optimum is in the wet "tundra". *Dryas* was found 200 ft. above the highest *Salix* on the bare shingle ridge of Mount Campbell (see Appendix).

The absence of *Carex rupestris* from the small part of the inner beach which was sampled is of no significance, since its distribution is very local, and it was found plentifully on silted shingle farther inland. It occurs in several wide patches on the outer beach, and seems to act, with *C. misandra* and *Polygonum viviparum* (in that order of sensitiveness), as an indicator of slight local increases in soil moisture in the unsilted shingle.

Development on the outer shingle beach.

The cold northerly wind may exert a slightly greater limiting influence on the vegetation on the promontory than on the beach just behind. Salt spray and occasional flooding, such as was observed when a large ice fall from the glacier occurred at high tide, might prevent the growth of land plants on the first few yards of the shingle beach, but on the exposed side of the beach, where the sea is encroaching on it, the vegetation goes to the edge.

It seems clear that the completely bare tip of Cape Napier is newly formed shingle in process of colonization, and the sequence of plants, e.g. along the line W (see Figs. 2, 3) may be taken as developmental.

The vegetation is noticeably denser in the depressions and on the youngest part of the beach is confined to them. For about 40 yards from the north-eastern shore-line the hollows contain nothing but blown seaweed and driftwood, but they are frequented by birds, especially purple sandpipers. Colonization of these hollows may be due partly to the birds and partly to the southerly wind which blows along the raised beaches carrying with it plant debris, sheets of dried blue-green algae, and frothy masses of plankton off the larger pools.

The first colonizer of the hollows is usually *Cochlearia officinalis* L. var. *arctica* (Schlecht.) Gel., which in some of them was found alone, but more often with *Swartzia inclinata* (M 1). In the depression at W 1 (see Fig. 3 and Pl. III, phot. 2) *Cerastium alpinum* L. and *Sagina intermedia* Fenzl. are also present, in addition to dead remains of *Saxifraga caespitosa* and *S. oppositifolia*. The next hollow which contains living vegetation is 32 yards farther south, but

thereafter every depression is colonized. Lichens do not appear till W 3, and living *S. oppositifolia* till W 4 (42 yards from W 1).

After W 5 (52 yards) the lichens begin to cover the shingle between the depressions, and by W 7 (82 yards) the lichen cover is complete. Here appears the belt of stunted *Salix polaris* which was mentioned previously, 10 yards in advance of the first *Dryas*. Thereafter, the vegetation takes on the appearance of typical *Dryas* "fjaeldmark" (see Pl. III, phot. 3), and the composition remains unchanged until at about W 14, with the addition of *Carex rupestris*, *C. misandra*, *Polygonum viviparum* and *Pedicularis lanata*, it appears to reach the edaphic climax on unsilted shingle, for on the continuation of the dry shingle beach beyond pools VI and VII it has not developed any farther.

At 16 A-17 G (Fig. 2) there is a low bank, and in front of it a belt of *Carex rupestris* and *C. misandra* occupying a broad shallow depression (see foreground of Pl. III, phot. 1). Finally, as the border of pool VI is approached, *Salix* replaces *Dryas*, mosses increase in frequency, and the typical plants of the wet "tundra" appear at the pool margin.

(ii) Salt marsh

The amount of vegetation on the mudflats which is subject to tidal inundation is very small, and is limited to zones bordering the pools, streams and tidal channels on the inner and middle mudflats. Fifty ring samples on the inner mudflat gave the following percentage frequencies:

Table II

C 1	70
<i>Puccinellia phryganodes</i>	16
M 1a (<i>Swartzia inclinata</i>)	14
<i>Enteromorpha</i> sp.	10

The most frequent order of colonization appears to be Cyanophyceae, *Puccinellia*, *Swartzia*, although in many places both *Puccinellia* and *Swartzia* are found colonizing the bare mud. On the silt, above the level of normal high tides, is a zone of almost pure *Carex subspathacea* which, beyond the tidal influence, gives place to wet "tundra" in which it is still dominant.

On the surface of the mudflats the Cyanophyceae form a skin (Pl. IV, phot. 5) which is coarsely wrinkled when dry and is readily colonized by *Puccinellia*.

There seems sufficient evidence to show that *Puccinellia* has spread considerably since Walton's survey, particularly on the middle mudflats in the region 4 G-3 L (Fig. 2). It is now established both on the previously bare "pan" of pool II, and just behind the outer shingle spit (Fig. 2, 2 D, 2 E), which was said by Walton to be "destitute of vegetation". It has not been seen in flower in the Bruce City district, but it spreads rapidly by stolons rooting at the nodes.

When specimens of *Puccinellia* were gently washed in a pool to remove mud, many small side shoots were seen to come away very easily, each breaking off at a node with one or more fine roots attached. These shoots floated down tidal channels, eventually lodging on the sides. This is probably the chief mode of dispersal of *Puccinellia*, which accounts for its spreading far in advance of other plants, and for the establishment of isolated plants along the edges of all the streams and tidal channels which flow from a zone where it is established.

It is evident from its establishment on the middle mudflats that *P. phryganodes* can withstand frequent tidal inundations. It is not found bordering fresh-water pools, but it does occur on a shingle bank just above the tidal level where it adopts a coarser and more upright habit. However, in a similar system of tidal pools enclosed by a spit on the west side of Petunia Bay, which is fresher than Adolf Bay, *Puccinellia* was found only at one point in minute amount, and the first colonizer is *Swartzia inclinata* which forms a very distinct zone outside the *Carex subspathacea* zone.

On the Cape Napier mudflats *Swartzia* has a secondary role as a colonizer, although it seems to be spreading on the middle mudflat at 4 K (Fig. 2). It has, however, a much wider range than *Puccinellia*, since it is found both on the shingle and on the silted area, though not, in general, far from the tidal limits.

Unlike these plants, *Carex subspathacea* does not survive below the limits of normal high tides, but it is an important colonizer of the edges of the mudflats, where it forms an almost pure zone, with, however, in some places the mosses *Swartzia* and *Bryum nitidulum* (M 1b). On the south-east side of the inner mudflat there is a considerable depth (a foot or more) of pure *Carex subspathacea* peat under the zone of the same plant, which shows that it has been long established there, and has kept pace with heavy silting.

The thin bands (1-2 in.) of *Carex* (probably *subspathacea*) peat found by Walton below the surface of the inner mudflat just north of pool IV were interpreted by him as showing that the plant had been overwhelmed by heavy silting from time to time, but it seems more probable that it was killed by excessive tidal inundation, particularly as the peat alternates with bands of organic matter thought to be derived from Cyanophyceae and diatoms which grow on the mudflats well within the tidal limits.

From the appearance of the rhizomes, *Carex subspathacea* seems able to colonize rapidly the bare non-saline mud, e.g. of a fresh "polygon mark" in the wet "tundra", but on the borders of the mudflats it spreads very slowly, forming a dense mat of branching rhizomes. A close comparison of the maps shows, however, that since 1921 the *Carex* zone has encroached slightly in many places, particularly on the south-east side of the mudflats, at 7 H and 4 H-L (Fig. 2).

There is evidence of more rapid spreading in the establishment of several small isolated patches on the north-west side of pools II and III, where further silting has occurred since 1921. As the shoots are far from brittle the method

of dispersal is probably by the fruits, which were found in moderate numbers on the south-east side, and would tend to be deposited in those places after exceptionally high tides.

Near the stream on the east side of the area, *Dupontia Fisheri* R.Br. is well established, and in some places is spreading on to the mud or shingle within the limits of the tidal influence. This grass, however, can scarcely be regarded as a normal constituent of the salt marsh, for it is not found away from the influence of fresh water, but its presence here indicates that, after *Carex subspathacea*, it has a greater tolerance of salinity than any of the other plants of the wet "tundra".

(iii) Wet "Tundra"

From the slopes of the Campbell range about a mile away the vegetation on the heavily silted area, which lies between the outer and the inner raised beaches, is clearly distinguishable by the rusty colour of its dominant plants, *Carex subspathacea* and the mosses of the M 2 complex.

Closer examination shows that a drier and a wetter part can be distinguished at sight by the prominence of the grasses *Dupontia Fisheri* in the wetter, and *Deschampsia borealis* (Trautv.) Roshev. in the drier region. That the differences are more extensive than this, however, is shown in Table III, which gives percentage frequencies based on fifty ring samples on each zone and over the whole silted area, separately.

Table III

	Whole wet "tundra" area	Wet "Tundra" I (with <i>Dupontia</i>)	Wet "Tundra" II (with <i>Deschampsia</i>)
M 2	92	84	94
<i>Carex subspathacea</i> Wormsk.	90	100	78
C 2	66	82	40
<i>Salix polaris</i> Wg.	57	28	88
<i>Equisetum arvense</i> L. var. <i>alpestre</i> Wahlb.	53	6	80
<i>Dupontia Fisheri</i> R.Br.	35	70	4
<i>Polygonum viviparum</i> L.	32	18	48
<i>Deschampsia borealis</i> (Trautv.) Roshev.	26	14	40
<i>Juncus biglumis</i> L.	19	26	4
<i>Carex parallela</i> (Laest.) Sommerf.	14	0	30
L 1	13	0	42
<i>Eriophorum Scheuchzeri</i> Hoppe	10	8	0
<i>Carex incurva</i> Lightf. var. <i>setina</i> Christ.	8	0	14
M 1b	6	12	6
<i>Carex misandra</i> R.Br.	4	2	2
<i>Saxifraga oppositifolia</i> L.	+	—	2
<i>Eriophorum angustifolium</i> Rott. f. triste Th.Fr.	+	+	+
<i>Saxifraga Hirculus</i> L.	+	—	+

The table reveals that, in addition to the conspicuous whitish tussocks of *Deschampsia*, the drier zone is characterized by high frequencies of *Salix*, *Equisetum*, *Polygonum* and lichens, and the wetter zone, in addition to *Dupontia*, by Cyanophyceae, of which the brownish gelatinous lumps (mostly *Nostoc* spp.) cover a large part of the surface. *Juncus biglumis* (from which the rarer *J. triglumis* was not distinguished in the field) is frequent in the wetter

zone, and the cotton grasses, though relatively infrequent, when in flower are the most obvious constituent of it.

The frequency of eight recorded for *Eriophorum Scheuchzeri* in the *Dupontia* zone is too low. The tendency for it to grow in small dense isolated patches no doubt accounts for its "unfair" sampling. However, *Eriophorum* is not an important constituent of the vegetation on the silted area except towards the south-east side.

Boggy places in the *Dupontia* zone are indicated on the map (Fig. 2), but probably vary from year to year and seem to have little significance for the vegetation. In some of the wettest *Drepanocladus revolvens* (Sw.) Warnst., was found along with the other *Hypnum* mosses which dominate the whole silted area, but there is no *Hypnum* moss bog in the area of sufficient size to take account of except near pool IV at 9 G, and the *Eriophorum* is widely scattered in small clumps and forms no extensive bog community such as is found further inland.

The slightly lower frequency of the M 2 mosses in the *Dupontia* zone is due to the presence of fresh "polygon marks" there. The frequencies of *Carex subspathacea* and *Dupontia* are not affected because their rhizomes enable them to colonize the bare mud much more rapidly than the mosses.

On the actual site of Walton's pool V there are now several such "polygon marks", 3-4 ft. in diameter, consisting of bare soft mud recently colonized by *Carex* and *Dupontia*, with occasional clumps of moss. Round the edge is a firm raised rim, covered with a dense mat of moss, *Carex*, *Dupontia*, *Salix* and *Polygonum*. Such a "polygon mark" has evidently been formed recently, and the centre is often so soft that it can be trampled down to a depth of 18 in. or more.

A succession can be traced from this type of young "polygon mark" to the old "polygon marks" which are found on the drier part of the silted area (see Pl. IV, phot. 6). In these the centre is hard and is fully colonized by *Carex subspathacea*, mosses and *Salix*, and often a grey lichen crust (L 1). The rim is larger in proportion and is densely covered with *Salix* (which grows up through the mosses), *Deschampsia*, and *Equisetum*. In places the rims of old "polygon marks" form an irregular network of ridges.

It seems unlikely, however, that the somewhat similar markings on the inner mudflats "may be indications of a similar action to that which produces 'Polygon Marks'" (Walton, 1922, legend to Pl. VII, fig. 1). They are for the most part smaller, deeper, more variable in size, and are filled with water from below at every tide through cracks in the bottom. It would seem probable that they are formed chiefly if not entirely by water action.

TRANSITIONAL AREAS

Within the area studied transitions occur between all three main communities, and the distribution of plants across them is shown by the frequency transects as follows:

Salt marsh to Fjaeldmark I	frequency transect	X 1-38 (Figs. 2, 4)
Fjaeldmark I to wet "tundra"	" "	Y 1-4 (Figs. 2, 5) and
		W 18-21 (Figs. 2, 3)
Salt marsh to wet "tundra"	" "	Z 1-10 (Figs. 2, 6)
Wet "tundra" to Fjaeldmark II	" "	Z 17-20 (Figs. 2, 6)

THE SHINGLE BANK

Between the outer beach and the Pool Area is a steep bank of shingle, from 3 to 7 ft. in height except at the ends where it tapers out. The slope is variable, and is more gentle opposite the shingle laterals.

By comparison with the vastly greater system of shingle laterals at Blakeney Point (Salisbury, 1922) one would expect that the proportion of fine particles in the soil, and the organic content, would increase from the newest to the oldest part of the system, and the carbonate content would decrease owing to leaching. The first two expectations were readily confirmed by observation, but the third was not, as the situation is complicated by the presence of ground-ice and the occurrence of soil convection in the spring owing to the irregular thawing of the snow. Calcareous nodules on the surface in some places provide evidence of the upward movement of soil water.

The bank is crossed by the transect lines X and Y, and the vegetation was also sampled at the point U and V opposite the shingle laterals. Table IV gives an indication of the composition on the bank at four points. As might be expected, the proportion of wet "tundra" plants increases as one passes from north to south.

Table IV

(Frequencies based on 10 ring samples)

Point of sampling	X 30	U	Y 2	V
Map ref. (Fig. 2)	7 C	9 E	11 E	13 K
L 6	9	4	10	—
L 2	9	3	6	—
M 1 b	3	—	—	—
<i>Salix polaris</i>	1	2	10	5
<i>Saxifraga oppositifolia</i>	1	3	10	—
<i>Cladonia pyxidata</i> f.	1	—	—	—
<i>Draba alpina</i>	+	1	—	—
<i>Saxifraga caespitosa</i>	+	—	—	—
<i>Dryas octopetala</i>	—	4	4	4
M 4	—	1	2	—
<i>Equisetum arvense</i> f.	—	—	7	8
<i>Polygonum viviparum</i>	—	—	4	4
<i>Cetraria nivalis</i>	—	—	1	—
<i>Carex misandra</i>	—	—	—	7
<i>C. subspathacea</i>	—	—	—	5
<i>Juncus biglumis</i>	—	—	—	4
<i>Deschampsia borealis</i>	—	—	—	3
<i>Carex incurva</i>	—	—	—	2
<i>Luzula nivalis</i>	—	—	—	2
<i>Saxifraga Hirculus</i>	—	—	—	+

THE SHINGLE LATERALS

Of the four shingle bars the outermost (Fig. 2, 1 D-2 H) is still quite bare, although *Puccinellia phryganodes* is established in the mud just behind it.

The second, between the middle and inner mudflats (4 D-5 J) is also bare, except at its highest point, the bank at 5 H, which has been colonized by L 1, *Salix polaris*, *Stellaria humifusa* Rottb., *Puccinellia Vahlia* (Liebm.) Scribner & Merrill, and *Potentilla pulchella* R.Br. Of these only *Salix* and *Potentilla* were listed by Walton (p. 118) as being at this point in 1921, and *Cochlearia* and *Draba*, both recorded then, were not seen there by me in 1936, so that a slight development has taken place in the replacement of these pioneers by other plants. Also the zones of *Puccinellia phryganodes*, *Carex subspathacea* and *Dupontia Fisheri*, which now almost encircle this bank on the mud, have slightly encroached on the shingle in several places.

The third shingle lateral lies south of pool III (9 E-9 G) and also has zones of the salt-marsh plants at its base. The shingle on the slope has a polygonal formation, the centres of many of the polygons being bare, and often showing calcareous nodules. Most of this slope is covered with a *Dryas-Salix*-lichen community of the type recorded at U (Table IV). Lower down on the tips of the shingle spur (e.g. at 9 G) *Puccinellia Vahlia* was found, with *Carex misandra* and *Cyanophyceae* (C 2). The dampness of the shingle here is due to the presence of the spring at 9 F and the wet moss bog at 9 G.

The fourth shingle bar at 12 K completes the series. The vegetation here is intermediate between the fjaeldmark of the silted inner beach into which it merges, and the drier zone of the wet "tundra". The composition is shown at V (Table IV).

There seems to be evidence of a succession on these shingle banks which differs from that on the main beach. Of three plants which are restricted to them within the area studied, *Potentilla pulchella* was found elsewhere only on or near stream estuaries, *Puccinellia Vahlia*, of which a few plants have established themselves on the mudflats and adjoining shingle, was also found in profusion on the Campbell range a mile away, but not intermediately, and *Luzula nivalis*, which was reported by Walton as frequent on the silted area, is now restricted to a small patch round V, but is plentiful in damp communities on the upper raised beaches.

COMPARISON WITH WALTON'S ZONES

(a) *Zonation from Pool Area to outer shingle beach* (see Walton, p. 115)

The frequency transect X (Figs. 2, 4) crosses Walton's zones from the edge of pool III to the top of the shingle bank, at the place investigated by him in 1921.

Zone 1, *Enteromorpha* with "*Glyceria vilfoidea*", has spread considerably,

and in addition, at the edge of the pool, mixed with the *Enteromorpha*, there is now a zone of *Rivularia* sp. forming black spots on the stones.

Zone 2, *Bryum* sp. with *Enteromorpha*, is not now to be found here, this part of the ground being now colonized by *Glyceria*, which extends up to and beyond the highest drift line. Comparison of Walton's map with my Fig. 4 shows that the *Glyceria* zone has expanded at this point from about 3 ft. in 1921 to approximately 12 ft. in 1936.

Zone 3 (Walton's *Distichium-Stereodon* zone) is now occupied by a broad belt of mosses (M 1b) and sterile lichens (L b) covered with Cyanophyceae which no longer form "occasional globules" but give the whole zone a black appearance.

The moss *Stereodon Vaucheri* (Lesq.) Lindb. is not now to be found there, and the lichens are unrecognizable, but a distinct band of *Cochlearia officinalis* is present in the zone.

Of pool II Walton states: "There is no apparent vegetation close to it, and the first zone to appear seems to be the *Distichium-Stereodon* Zone, succeeded by the shingle bank flora." The mud pan of this pool is now covered with Cyanophyceae (C 1), and around it is a definite zone of *Puccinellia phryganodes* which is established on the mud pan in several places. At the north-west end is a patch of *Carex subspathacea*. There is therefore direct evidence of the appearance of these plants since 1921.

Zone 4 is given as "slope of shingle with *Saxifraga oppositifolia*. . . *Dryas octopetala*. . . *Stereocaulon paschale*". Of these, only the first appears now, near the top of the bank with *Salix polaris*, the steep part of the slope being occupied chiefly by lichens and a very few isolated pioneer shingle plants.

Finally, the list given by Walton for zone 5 (top of main shingle beach) evidently refers to the beach as a whole, since few of these plants are found near the bank opposite pool III. *Papaver radiculatum*, however, is not now found on the beach nearer than Bruce City, and the dominant lichen on shingle throughout the district is *Lecanora epibryon* (Ach.) Ach., not *L. tartarea* as listed both by Walton and Summerhayes & Elton (1923). No *L. tartarea* was collected by me from the shingle beach, and an examination by Mr I. M. Lamb of Walton's original specimen showed that it had been wrongly named, and that it also was, in fact, *L. epibryon*.

Of the changes which have occurred since 1921 on this piece of bank, the chief are: spread of the "*Glyceria* zone" up the bank, no doubt due to further silting, great increase in Cyanophyceae, an indication of increased dampness, appearance of *Cochlearia* near the middle, and *Salix polaris* near the top of the bank, disappearance of *Stereodon Vaucheri* and *Dryas* from zones 3 and 4 respectively.

The transition from shingle beach to pool V is shown along the line Y (Fig. 5). Walton's moss zone E (chiefly M 4) and *Dryas* zone (D), are recognizable, but the complete filling up of the pool and the formation of "polygon

marks" on it, are the only changes which can be established with certainty. A black belt of dense Cyanophyceae (chiefly *Rivularia* sp.) lies on the shingle between the bank and the bog (at Y 3).

(b) Zonation on south-east side of Salt Marsh

The line Z (Figs. 2, 6) traverses the zones mapped by Walton on this side. It enters zone I (*Glyceria-Enteromorpha*) at Z 4. Z 6 is well inside zone II—" *Carex salina* . . . and a certain amount of moss (probably *Bryum nitidulum* Lindb.) *Dupontia Fisheri* ". The moss at this point, however, is mostly *Swartzia* with a little *Bryum*, and *Dupontia* does not appear till Z 8. The *Carex* appears to have encroached upon the mudflat here a little.

In zone III, states Walton, "*Carex salina* . . . is gradually dominated by: *Eriophorum Scheuchzeri* Hoppe, *Luzula hyperborea* R.Br., *Eriophorum polystachyum* L." There is now no sign of this zone. *Carex subspathacea* remains more or less dominant over the whole silted area, *Luzula* is absent, and the cotton grasses are very infrequent, except on the further side, near the inner raised beach.

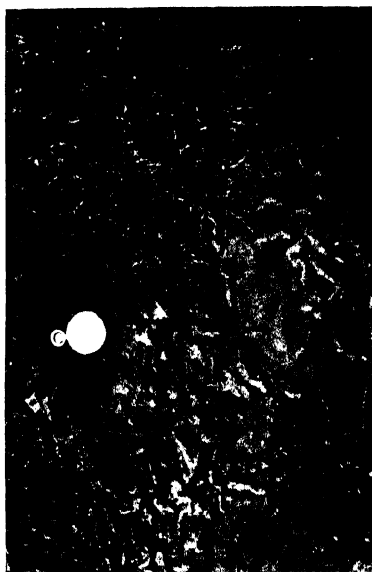
At Z 10 the line enters zone IV, which is clearly marked by the appearance of *Salix* and other wet "tundra" plants. Mosses of the M 2 complex replace M 1 and remain co-dominant with *Carex subspathacea*, over the whole silted area. Walton writes, however (p. 116) "The silting apparently inhibits to a large extent the growth of mosses", and among plants which predominate on the tussocks he gives—*Luzula hyperborea*, *Stellaria longipes* Goldie, *Saxifraga Hirculus* L.—which are now absent, except the last, which is infrequent.

At Z 18 (Fig. 2, 8 L) is a bare belt covered with greyish lichens (L 1 and L 6) with a few plants only of *Cochlearia* and *Deschampsia*, which forms an abrupt transition from the wet "tundra" to Fjaeldmark II.

No mention is made, either by Walton or Summerhayes & Elton, of the conspicuous grass *Deschampsia borealis*, and it is possible that it has increased greatly in prominence, or even that it is a newcomer to the district.

From the above evidence it would seem that *Carex subspathacea* and the M 2 mosses have spread since 1921 across the silted area from zone III onwards, to the exclusion of many plants formerly present.

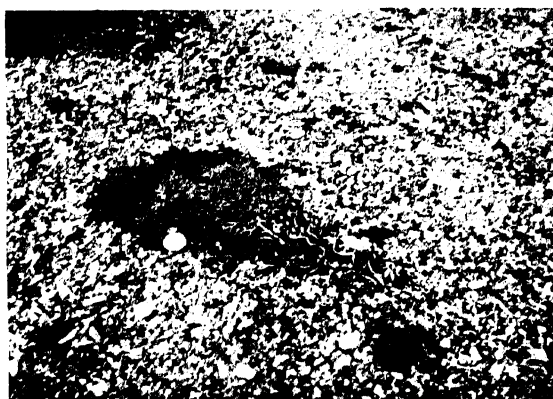
It is difficult, however, to draw conclusions about changes on this side of the mudflat, because Walton's map is less definite here, and does not extend to the inner raised beach. Sampling with a small ring tends to show up the prominence of inconspicuous plants such as *Carex subspathacea* as compared with those having conspicuous flowers (e.g. *Eriophorum*, *Saxifraga Hirculus*) which are liable to be over-estimated by eye. In the region Z 10–13 (Fig. 6) the dense tussocks of *Salix* make the presence of *Carex subspathacea* not at all obvious, but the ring shows a frequency of 60–80 %, and even this is likely to be an under-estimate, as it is impossible, without picking each tussock to pieces, to be sure that it does not contain rhizomes of *Carex*.



Phot. 5. Surface of inner mudflat showing wrinkled film of Cyanophyceae and plants of *Puccinellia phryganodes*.



Phot. 6. Fresh mud "polygon mark" in wet "tundra." In background, older, fully colonized "polygon marks."



Phot. 7. Effect of northerly winds on tussock of *Dryas*. The shingle round it is covered with lichens.

Although, therefore, it is not safe to conclude that *Carex subspathacea* has spread greatly since 1921, the evidence is clear that *Luzula* and *Stellaria longipes* have disappeared from the silted area since then, that *Saxifraga Hirculus* has decreased greatly in amount, and that the cotton grasses have retreated considerably from the part towards the mudflat. All these are moisture-loving plants found on pool or stream margins inland, and their decrease or disappearance, taken in conjunction with the filling up of pool V and the presence of several small dried up pools on the farther side of the silted area (Fig. 2, 10-11 L) shows that this area is drier than in 1921, and that the effect is due to more than seasonal variation.

CONCLUSION

In the Bruce City region there are no extensive barren communities such as those described by Trapnell (1933) in south-west Greenland. Nearly all the higher plants flower and fruit profusely, but there is no sign of the abundance of seedlings recorded by Wagner (1938) in east Greenland. In fact, despite close examination of the ground in the sampled areas, remarkably few seedlings were seen at all, and on the dry fjaeldmark none, except seedlings of *Dryas* among the leaves of old tussocks, and of a few pioneer plants such as *Cochlearia* in the depressions. It is clear that under these conditions regeneration and development must be extremely slow.

However, there is now sufficient evidence of succession to make it seem unlikely that the two series, on the shingle beach and on the silted area, respectively, are converging towards a Cassiope Heath or other climax community, as suggested by Walton (p. 117), and in view of the further evidence provided, it is necessary to modify his tentative plan (Walton, Fig. 6).

On the shingle beach behind Cape Napier there is no indication that the development will pass beyond the stage of Fjaeldmark I with *Dryas*, *Saxifraga oppositifolia* and lichens on the ridges, and, in addition, *Carex rupestris*, *C. misandra* and *Pedicularis lanata* in the depressions. There is no evidence of silting of this beach, although, should it occur, one would expect the new succession to proceed as far as Fjaeldmark II, with *Salix*, *Deschampsia*, *Polygonum*, etc.

On the other hand, on the mudflats direct evidence confirms the succession as far as the *Carex subspathacea* zone.

Beyond this the situation is complicated by the intervention of fresh water, and the course of new successions will depend upon the direction taken by the streams and the drainage of the soil water, but the indications are that *Dupontia Fisheri* will become established along stream margins, even near the tidal limits. If silting continues, the *Carex-Dupontia* zone may be colonized by *Eriophorum* and mosses, and finally by *Salix* and other plants, forming pool—or bog—marginal (wet "tundra" I) communities, and finally, if silt accumulates and the water level falls, the area may dry out, as the silted area on the south-

east side of the inner mudflat appears to be drying now, and may give rise to wet "tundra" II, and possibly in time to a type of polygonal clay fjaeldmark.

However, the scope of this investigation is too limited to give any reliable indication of the general ecology of the district and in the following plan of the successions the speculative later stages have been omitted.

Sea

Bare shingle with depressions containing seaweed and other debris	Bare tidal mud
(depressions only)	Cyanophyceae (C 1)
Pioneers—especially <i>Cochlearia</i>	<i>Puccinellia phryganodes</i>
	<i>Swartzia inclinata</i> (M 1a)
(ridges and depressions)	<i>Carex subspathacea</i> with <i>Swartzia</i> and
"Open" community of <i>Saxifraga oppositifolia</i> and lichens (chiefly <i>Lecanora epibryon</i>)	<i>Bryum nitidulum</i> (M 1b)
Lichens become "closed"	(Intervention of fresh water)
<i>Dryas</i> "fjaeldmark" with <i>Saxifraga oppositifolia</i> and closed lichen community	As above with <i>Dupontia Fisheri</i>
(depressions only)	?
As above, with addition of <i>Pedicularis lanata</i> , <i>Carex rupestris</i> , <i>Carex misandra</i>	

APPENDIX

Plants found on Mount Campbell at about 2000 ft.

Summerhayes & Elton (1923) give a list of plants found up to 500 ft. on the Campbell Range, and remark (p. 264) that "*Saxifraga oppositifolia* is the only plant occurring at 2000 ft. in this area".

It is of interest, therefore, to record the finding of a number of other plants at a height estimated at about 1800 ft. on the actual summit of the ridge, though not at its highest point. All the following plants were collected within an area of a few square yards on the top of the ridge, at a point where it is only a few yards wide, but is protected to some extent from the north and east by the slightly higher part opposite Bruce City. No other vegetation except *Saxifraga oppositifolia* and lichens was seen above or for some distance below this point, either on the ridge itself or on the screes forming the sides.

Angiosperms:	<i>Cerastium</i> sp. (probably alpinum)
	<i>Draba alpina</i> L.
	<i>Dryas octopetala</i> L.
	<i>Minuartia rubella</i> (Wahlenb.) Hiem.
	<i>Papaver radicans</i> Rottb.
	<i>Phippsia concinna</i> Lindb.
	<i>Puccinellia Vahlana</i> (Liebm.) Scribner & Merrill
	<i>Saxifraga oppositifolia</i> L.
Lichens:	<i>Aspicilia</i> sp.
	<i>Lecanora epibryon</i> (Ach.) Ach.

SUMMARY

1. The area at Cape Napier which was described and surveyed by Walton in 1921 has been reinvestigated. The vegetation has been studied in greater detail by the use of a method of ring sampling which is described, and its composition is recorded, with the aid of a vegetation map based upon a plane-table survey, and of "frequency transects" across the transition areas.

2. The three chief plant communities in the area are: *Dryas* "fjaeldmark" on shingle, "salt marsh" on the tidal mudflats and wet "tundra" on the silted area above the tidal limits.

3. Changes which have occurred since 1921 include: further colonization of the mudflats by the salt marsh plants, especially *Puccinellia phryganodes*, filling up of pool V, and changes in vegetation which indicate that part of the silted area is slowly drying out.

4. The dominant lichen on shingle is found to be *Lecanora epibryon* (Ach.) Ach., and not *L. tartarea* Ach. as previously recorded.

5. Modifications are suggested in the scheme of succession put forward by Walton (1922).

6. A note on plants found at a high altitude on the Campbell range is included in an appendix.

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Cryptogams: at the British Museum (Natural History).

Mosses: W. R. Sherrin.

Lichens: I. M. Lamb.

Cyanophyceae: R. Ross.

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REFERENCES

- Elton, C. S. & Baden-Powell, D. F. W. "On a collection of raised beach fossils from Spitsbergen." *Geol. Mag.* **68**, 385-405, 1931.
- Johnson, D. W. *Shore Processes and Shoreline Development*, Chap. ix. London: Chapman and Hall, 1919.
- Oliver, F. W. "The shingle beach as a plant habitat." *New Phytol.* **2**, 73-99, 1912.
- Raunkaier, C. *The Life Forms of Plants and Statistical Plant Geography*. Oxford, 1934.

- Salisbury, E. J.** "The soils of Blakeney Point: a study of soil reaction and succession in relation to plant covering." *Ann. Bot., Lond.*, **36**, 391-431, 1922.
- Summerhayes, V. S. & Elton, C. S.** "Contributions to the ecology of Spitsbergen and Bear Island." *This JOURN.* **11**, 214-86, 1923.
- Summerhayes, V. S. & Elton, C. S.** "Further contributions to the ecology of Spitsbergen." *This JOURN.* **16**, 193-268, 1928.
- Trapnell, C. G.** "Vegetation types in Godthaab Fjord." *This JOURN.* **21**, 294-334, 1933.
- Wager, H. G.** "Growth and survival of plants in the Arctic." *This JOURN.* **26**, 390-410, 1938.
- Walton, J.** (1922). "A Spitsbergen salt marsh; with observations on the ecological phenomena attendant on the emergence of land from the sea." *This JOURN.* **10**, 109-21, 1922.
- Warming, E.** *Oecology of Plants*. Oxford, 1909.

THE OCCURRENCE OF BURIED VIABLE SEEDS IN SOILS AT DIFFERENT ELEVATIONS AND ON A SALT MARSH

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THE investigations conducted at the Welsh Plant Breeding Station on the buried viable seed content in soils of lowland grassland, the cultivated fields of hill farms and natural hill pastures (1, 2) have entailed the study of soil samples for this purpose from numerous habitats and degrees of elevation above sea-level. The highest land which came under investigation was a sheep walk with a range of elevation from 1500 to 1850 ft. The soil from beneath each type of plant association on this land was found to contain viable seeds.

It was considered that interesting results would be obtained if soil samples were taken at successive elevations and subjected to buried seed analysis, and in the spring of 1936 an investigation was commenced with this object. The buried viable seed content of a salt marsh was investigated at the same time, and the results are here incorporated.

The slopes chosen for the elevation samples were situated on Plynllymon, Cardiganshire and Cader Idris, Merionethshire, while the salt-marsh samples were taken on the Dovey salt marshes in North Cardiganshire. A number of areas representative of the herbage communities were sampled on the mountains and on the marsh. The method of sampling these representative areas and the subsequent treatment of the soil for its seed content have been fully described in a previous paper (2). In brief the method of sampling consisted of taking fifty borings with a borer seven inches long (inside diameter of $1\frac{1}{4}$ in.) over an acre of uniform sward, care being taken to exclude contamination from surface seeds. The soils were under investigation for eighteen months.

RESULTS

Plynllymon. This mountain was sampled on the south side, and on a line from the lead mine to the summit. The seedlings which arose from the soil of the six areas sampled are given in Table I.

The first Plynllymon area was at an elevation of approximately 1600 ft. above sea-level and the chief components of the grass and miscellaneous herb population of the sward in order of abundance were: *Nardus stricta*, *Juncus squarrosus*, *J. communis*, *Vaccinium Myrtillus*, *Scirpus caespitosus*, *Carex* spp., *Erica cinerea*, *Potentilla erecta* and *Anthoxanthum odoratum*. As shown in Table I, the seedlings arising from the soil of this area were predominantly

Table I. The number of seedlings from the Plynllymon soil samples

Species	Ft. ... m. ...	Approximate elevation					
		1600 488	1800 549	1950 595	2100 641	2200 672	2400 733
<i>Sagina procumbens</i> Linn.	—	—	—	3	2	5	—
<i>Potentilla erecta</i> Hampe.	7	—	—	9	1	—	—
<i>Galium saxatile</i> Linn.	7	19	35	44	27	63	—
<i>Vaccinium Myrtillus</i> Linn.	5	—	—	—	—	1	6
<i>Narthecium ossifragum</i> Huds.	5	—	—	3	—	—	—
<i>Juncus communis</i> Mey.	119	85	56	5	—	—	2
<i>J. bulbosus</i> Linn.	5	2	11	—	—	1	—
<i>J. squarrosus</i> Linn.	66	31	107	51	17	15	—
<i>Luzula campestris</i> DC.	—	—	2	—	—	—	—
<i>Carex</i> spp.	63	25	62	45	98	5	—
<i>Anthoxanthum odoratum</i> Linn.	—	—	—	1	—	—	—
<i>Agrostis</i> spp.	—	17	16	43	3	—	—
<i>Deschampsia flexuosa</i> Beauv.	5	—	—	—	—	—	8
<i>Holcus lanatus</i> Linn.	—	1	—	—	—	—	—
<i>Molinia caerulea</i> Moench.	1	—	—	—	—	—	—
<i>Poa annua</i> Linn.	1	1	—	—	—	—	—
<i>Festuca ovina</i> Linn.	2	—	3	1	2	2	—
<i>Nardus stricta</i> Linn.	—	—	1	1	—	—	—

those of *Juncus* and *Carex*. Four species of grass were represented, but *Nardus* was absent although this species was prominent in the sward. The only seedling of *Molinia* occurred from this area.

The sward at 1800 ft. consisted of *Nardus stricta* and *Galium saxatile* as dominants. Other species present were *Luzula campestris*, *Juncus squarrosus*, *Agrostis* spp., *Anthoxanthum odoratum*, *Vaccinium Myrtillus* and *Polygala vulgaris* L. The seedlings which arose from this soil largely consisted of the *Juncus* and *Carex* group, but there were more seedlings of *Galium saxatile*, and a large number of *Agrostis* seedlings. A seedling of *Holcus lanatus* also occurred.

At 1950 ft. the sward was very similar in composition to that at 1800 ft. The seedlings from the soil sample consisted of the appearance of *Sagina procumbens* and of *Nardus stricta*, and it was here that *Luzula campestris* was seen. There was a very large number of *Juncus squarrosus* seedlings, but the *J. communis* seedlings were fewer compared with the lower samples.

The sward at 2100 ft. consisted chiefly of *Nardus stricta*, *Agrostis* spp., *Galium saxatile* and *Juncus squarrosus*. *Anthoxanthum odoratum* was one of the dominant grasses, but it occurred in patches. The seedlings from the soil are in agreement with the composition of the sward with the usual exception that *Nardus stricta* was scarcely represented though dominant in the sward. The number of *Galium saxatile* seedlings had increased from the lowest sample area to this elevation, while the number of *Juncus communis* had markedly decreased, and the remaining *Juncus* species were less abundant. *Agrostis* species, on the other hand, gave their largest number from the soil of this area, and *Anthoxanthum odoratum* made its only appearance for this slope.

At 2200 ft. the species differed from those at lower elevations in that *Festuca ovina* was the dominant grass. *Vaccinium Myrtillus*, *Carex* species and *Nardus stricta* were present and there were traces of *Anthoxanthum odoratum*.

The sward was very open in regard to grasses and miscellaneous herbs and consisted very largely of moss. The most marked feature of the seedling population from this area is the number of *Carex* seedlings. The number of *Juncus* seedlings was still fewer and the small number of seedlings of *Agrostis* compared with the number from the soil at 2100 ft. was very marked. The same disparity in the relationship of the number of seedlings derived from buried seeds and the number of plants in the sward is observable for *Festuca ovina* in this area, as was the case for *Nardus stricta* in the lower elevations.

The highest area on Plynlymon was taken around the cairns and the immediate neighbourhood at approximately 2400 ft. The sward at the highest part consisted chiefly of *Festuca ovina* with *Vaccinium Myrtillus* and smaller quantities of *Galium saxatile*, *Deschampsia flexuosa* and *Agrostis* spp. A slight depression east of the ridge had a soil of deep peat, and here the herbage consisted almost entirely of *Juncus squarrosus*, *Vaccinium Myrtillus* and *Luzula maxima* DC. The most marked feature of the buried seed flora is that *Galium saxatile* gave its greatest number of seedlings for the slope from this area, and *Carex* species the smallest. Each main constituent of the sward was represented in the seedling population from the soil.

Cader Idris. This mountain was sampled on the south-east side from a position just beyond the tree limit on the slope which extends from Tal-y-llyn Lake to the summit plateau.

The seedling data are given in Table II.

Table II. *The number of seedlings from the Cader Idris soil samples*

	Approximate elevation						
Species	Ft. ... m. ...	1200 366	1400 427	1600 488	1950 595	2300 702	2600 794
<i>Viola canina</i> Linn.	---	---	2	---	---	---	---
<i>Ulex Gallii</i> Planch.	28	---	---	---	---	---	---
<i>Potentilla erecta</i> Hampe.	14	10	30	2	---	---	---
<i>Galium saxatile</i> Linn.	32	14	52	14	7	32	---
<i>Taraxacum officinale</i> Weber.	4	---	---	---	---	---	---
<i>Campanula rotundifolia</i> Linn.	---	10	---	---	---	---	---
<i>Vaccinium Myrtillus</i> Linn.	---	---	---	18	1	---	---
<i>Erica cinerea</i> Linn.	---	---	---	48	30	---	---
<i>E. Tetralix</i> Linn.	---	30	14	8	2	---	---
<i>Calluna vulgaris</i> Salisb.	---	4	---	196	375	3	---
<i>Digitalis purpurea</i> Linn.	104	---	2	---	---	---	---
<i>Veronica officinalis</i> Linn.	2	---	---	---	---	---	---
<i>Rumex Acetosella</i> Linn.	---	---	---	---	---	---	1
<i>Juncus communis</i> Mey.	4	14	34	---	1	1	---
<i>J. bulbosus</i> Linn.	---	18	4	---	---	---	1
<i>J. squarrosus</i> Linn.	---	32	90	4	6	39	---
<i>Luzula campestris</i> DC.	---	---	4	---	---	---	---
<i>Carex</i> spp.	12	72	80	32	44	---	---
<i>Anthoxanthum odoratum</i> Linn.	2	6	4	---	---	---	---
<i>Agrostis</i> spp.	40	82	56	4	3	7	---
<i>Deschampsia flexuosa</i> Beauv.	---	2	---	4	---	---	3
<i>Holcus lanatus</i> Linn.	---	---	1	---	---	---	---
<i>Triodia decumbens</i> Beauv.	---	2	---	---	---	---	---
<i>Poa annua</i> Linn.	2	---	6	---	---	---	---
<i>Festuca ovina</i> Linn.	2	4	34	4	3	---	---
<i>Nardus stricta</i> Linn.	---	2	---	---	1	---	---

The first sampling was taken on a *Festuca-Agrostis* pasture above the tree line and was at approximately 1200 ft. above sea-level. The sward consisted of *Festuca ovina* and *Agrostis* species as dominants, and associated plants were *Anthoxanthum odoratum*, *Potentilla erecta*, *Galium saxatile*, *Carex* species and *Digitalis purpurea*. The greatest number of seedlings given by a single species from this soil was by *Digitalis purpurea*. *Ulex Gallii* and *Veronica officinalis* appeared only from the soil of this area, and also a small number of seeds of the lowland species *Taraxacum officinale*.

At 1400 ft. the herbage consisted of a *Festuca ovina*, *Agrostis* and *Nardus* pasture. The soil was moister than at the lower area, and the chief miscellaneous herbs associated with the above grasses were *Erica Tetralix*, *Juncus squarrosus* and *Carex* species. The seedling population comprised large numbers of the *Juncus* and *Carex* species, and the number of *Agrostis* seedlings was exceptionally great. This soil provided the only appearance for the slope of *Viola canina*, *Campanula rotundifolia* and *Triodia decumbens*.

The sampling at 1600 ft. was taken on fairly level land adjoining Llyn Cau. The herbage was chiefly *Festuca ovina*, *Agrostis* species and *Nardus stricta*; associated plants were *Juncus squarrosus*, *Potentilla erecta*, *Galium saxatile*, *Anthoxanthum odoratum* and *Carex* species. The most noteworthy characteristic of the seedling population was the very large number of *Festuca ovina* seedlings which arose from this soil. This area had a greater number of buried viable grass seeds than any other on the slope, although the soil at 1400 ft. gave rise to more grass species. Large numbers of *Juncus* and *Carex* seedlings arose from the soil of the present situation.

The samplings at the next two elevations were carried out on the ridge which commences on the south side of Llyn Cau, and extends to the summit plateau. The herbage at 1950 ft. consisted chiefly of dense *Calluna vulgaris*, with *Erica* and *Carex* species associated with it. The seedling population is very largely composed of the species in evidence in the sward, and in the same order of dominance.

The sward at 2300 ft. was again chiefly composed of *Calluna*, and associated species were *Erica cinerea*, *Juncus squarrosus*, *Scirpus caespitosus*, *Vaccinium Myrtillus*, *Nardus stricta* and *Carex* species. The seedling population which was derived from the buried seeds of this area consisted of a great number of *Calluna vulgaris* with lesser numbers of *Erica* and *Carex* species. The number and species of grass seedlings were few, but it is interesting to note that *Nardus stricta* appeared from this soil as it had done from the soil of the 1400 ft. elevation, although at this latter height it had been one of the dominant species in the sward.

The highest soil sampling area was taken at approximately 2600 ft. and was situated on the plateau which extends to the summit of Cader Idris. The area consisted of a very short *Festuca ovina*—*Deschampsia flexuosa*—*Vaccinium Myrtillus* pasture situated between large stones. There was a little *Agrostis* and

Anthoxanthum present, and an occasional plant of *Rumex Acetosella*, while *Juncus squarrosus* was very plentiful and *Galium saxatile* and *Luzula campestris* were present to a lesser extent. The seedlings which arose from this soil were chiefly those of *Galium saxatile* and of *Juncus squarrosus*. No seedlings occurred of *Festuca ovina*, *Vaccinium Myrtillus*, *Anthoxanthum odoratum* or *Luzula campestris*, although the first two named species were dominant in the sward. It is interesting to note that a single seedling occurred each of *Juncus communis* and of *J. bulbosus*, and especially that one occurred of *Rumex Acetosella*.

DISCUSSION ON THE ELEVATION DATA

As the soil samples were taken at successive elevations on the slopes there were alterations in the plant associations to be expected, although several species occurred in the herbage from the lowest to the highest elevations sampled. The result for the majority of the species, however, is that they were not present in the herbage throughout the complete series of elevations which were sampled. With regard to the flora on Plynlymon and on Cader Idris the species present at different altitudes has been investigated by Salter (3), while Price Evans (4) has given a detailed account of the flora of the northern slope of Cader Idris. The observations on the main constituents of the herbage at different altitudes in the present experiment coincide with these writers, but mention is made by them of numerous miscellaneous herbs which were not observed to be components in the plant associations investigated in the present trial, nor did their seedlings arise from the soil samples. The reason for this is that many of these species grow in sheltered places on the mountains as is pointed out by these writers, and would, therefore, not have been in the main plant associations sampled for buried viable seeds.

It will be noted that whereas eighteen species gave seedlings from the Plynlymon soils, twenty-six occurred in the Cader Idris soils. The difference was chiefly in the miscellaneous herb group. The more numerous flora of Cader Idris compared with Plynlymon has been commented upon by Salter (3), and the factors which cause the variety of the Cader Idris flora have been enumerated by Price Evans (4). The number of *Juncus* seedlings which occurred from the soils of both slopes was considerable. Most of these seedlings were *J. squarrosus*, and as this species was a constituent of the swards throughout the series of elevations on both slopes, with a single exception on Cader Idris, it is evident that where this species is present in the herbage to any extent, large numbers of its seeds will be present in the soil beneath. The same relationship exists in the case of *J. communis* and *J. bulbosus*. Very little of these species was found growing above 2000 ft. and consequently the data show that soil samples taken above this altitude contained but few of their seeds. The Plynlymon data for *J. communis* indicate that there was a progressive decline in the numbers of its buried seeds from 1600 ft. upwards. *Luzula maxima* was plentiful in the sward at the top of Plynlymon, but no seedlings of this species

arose from the soil. Salter (5), in mentioning that *L. maxima* occurs at the summit of Plynlymon, also lists numerous situations over a wide range of elevations where it grows. No seedlings of *Scirpus* occurred from the soils of the slopes, although the plants of *S. caespitosus* were in evidence, particularly at the lowest elevation sampled on Plynlymon. Evidence of buried viable seed of *S. setaceus* was obtained in both the earlier investigations (1, 2), and of *S. caespitosus* in the second investigation. The data suggested, however, that this latter species relied chiefly upon vegetative means for perpetuating itself. The large number of seedlings of the *Carex* species and of *Galium saxatile* which arose from the soil samples rank with those of *Juncus squarrosus* in showing that buried seeds of these species are abundant throughout the elevations. With regard to the *Calluna* and *Erica* seedlings which arose from the Cader Idris soil samples, the two situations from which the greatest number occurred, were from areas on which these species dominated the sward. It was previously found (1) that the large numbers of buried viable seed of *Calluna* and *Erica* species were often out of proportion to the amounts of their plants in the sward. In the present instance, however, as the herbage at the two elevations in question was almost pure *Calluna* and *Erica* the discrepancy between the number of buried seeds of these and the remaining species, particularly the grasses, did not arise. With reference to the growth of *Calluna vulgaris* on Cader Idris, Price Evans (4) mentions that the optimum growth occurs at a lower elevation on the northern slope than was recorded for the dense areas sampled on the southern slope for the present trial. It is further mentioned, however, that *Calluna* occurs at the higher altitudes but in rather a dwarf form.

Of the grasses by far the greatest number of seedlings from the soils of both slopes were *Agrostis*. Little of these species occurred in the surface vegetation of either mountain in the higher elevations, and the data show correspondingly few buried seeds. The single addition to abundant buried viable seeds of a grass was given by *Festuca ovina* from the soil taken near Llyn Cau. The earlier work (1) pointed to the fact that most grasses rely upon vegetative means in order to perpetuate themselves. *Agrostis*, among others, was a possible exception to this behaviour. The subsequent investigation (2) suggested that *Festuca ovina* could be included as another exception, and the data for the particular area here under discussion confirm this. It is probable, however, that the moisture content of the soil is a controlling factor. The Llyn Cau area was a deep moist peat, and the data show that the largest number of buried viable seeds for five of the chief species occurred from this soil, as well as an exceptionally large number for *F. ovina*. On the other hand, *F. ovina* was the dominant species in the herbage at the highest elevations sampled on both mountains but there the soils were thin and dry in comparison, and few seedlings of this grass arose from the soil samples. This is in agreement with the earlier investigations (1, 2) where there were decided indications that more seeds are present in a viable condition in waterlogged soils. It is evident that at the highest altitudes

sampled *F. ovina* perpetuates itself chiefly vegetatively, but that *Agrostis* species and possibly *Deschampsia flexuosa* use seed production to a greater extent than *Festuca ovina*, judging by the relative proportions of these plants in the swards under discussion.

Few buried viable seeds of *Molinia caerulea* and *Nardus stricta* occurred in the soil samples. This was repeatedly observed throughout the earlier investigations (1, 2) notwithstanding the fact that these species were often the chief components in the surface vegetation. As has been previously pointed out and discussed (2), the data indicate that certain natural causes exist which prevent large quantities of their seed entering the soil and remaining in a viable condition. Coulon (6) mentions that the power of the germination of *N. stricta* seeds decreases with increasing altitudes, becoming nil above 2550 m., the reason being that the fruit does not develop at high altitudes. The number of seedlings of *Nardus* which arose from the soils here investigated, however, were too few to show any coincidence with this finding, and the elevations sampled are comparatively low compared with the figure quoted by Coulon. With regard to *Molinia caerulea*, Jefferies (7) states that the seeds germinate in cracks and hollows of the soil, and give rise to a great number of seedlings. It is evident, therefore, that with such marked surface germination few seeds remain to enter the soil.

It is extremely probable that seeds which enter the soil on the slopes of Plymlym and Cader Idris, and in fact all such country, remain in the top few inches of soil. It was found by the authors of the first experiment on this subject here referred to that a certain number of seeds in a viable state were present in worm casts (8). Viable seeds occurred below a depth of 12 inches in lowland soils when worms were plentiful, but in hill soils, where extremely few worms were found, the seeds were only in the top 3 inches of soil. In the present experiment the soil samples were all of the latter category.

The Dovey salt marshes. Five areas in the Treddol district of the Dovey Estuary were chosen for buried viable seed sampling. The first was a pasture adjoining the bare silt by the river, and the remaining four areas were successively farther inland and were only separated from one another by the railway line or by streams. The seedling data derived from these soils are given in Table III.

The first plant community consisted chiefly of *Glyceria maritima*, *Armeria maritima* and *Aster Tripolium* with the grass as dominant. *Salicornia herbacea* was growing on the silt adjoining the sward. This area was intersected by deep pans. The seedling data show the presence of viable seeds of the above three species forming the sward, and also of *Salicornia*. The abundance of the buried seed of *Glyceria* is in contrast to the numbers for the remaining species, especially of *Armeria*, which species was extremely prolific in the sward.

The second area was dominated by the tall growth of *Juncus maritimus*

Table III. The number of seedlings from the Dovey salt-marsh soil samples

Species	Areas				
	1	2	3	4	5
<i>Cochlearia officinalis</i> Linn.	—	—	—	1	—
<i>Sagina procumbens</i> Linn.	—	—	—	—	1
<i>Stellaria media</i> Vill.	—	—	—	—	1
<i>Spergularia rubra</i> Presl. var. <i>marina</i>	—	—	—	—	3
<i>Aster Tripolium</i> Linn.	1	—	—	—	—
<i>Carduus palustris</i> Linn.	—	2	—	—	—
<i>Glaux maritima</i> Linn.	—	—	15	1	32
<i>Anagallis arvensis</i> Linn.	—	—	1	—	—
<i>Samolus Valerandi</i> Linn.	—	8	—	—	—
<i>Galeopsis Tetrahit</i> Linn.	—	—	—	—	1
<i>Armeria maritima</i> Willd.	3	2	4	—	—
<i>Salicornia herbacea</i> Linn.	5	—	—	—	—
<i>Rumex obtusifolius</i> Linn.	—	—	—	—	1
<i>Urtica dioica</i> Linn.	—	—	—	—	1
<i>Juncus maritimus</i> Lam.	—	16	6	—	2
<i>Carex</i> species	—	8	—	—	—
<i>Agrostis</i> species	—	23	5	2	14
<i>Glyceria maritima</i> Mert. & Koch	25	—	28	—	30
<i>Festuca rubra</i> Linn.	—	2	2	1	5

which was interspersed with *Festuca rubra*, few other species being in evidence. An outstanding point in the seedling flora which arose from the soil was the large number of *Agrostis* seedlings, although few plants of these species were present in the surface vegetation. It is interesting that notwithstanding the thick surface growth of *Juncus* and *Festuca* the number of different species of seedlings from this soil was only exceeded by the number from the fifth area. As would be expected from the amount of *Juncus maritimus* in the herbage, the buried seeds of this species were more numerous in the soil than from the remaining areas in which *Juncus* was less plentiful.

The third sampling situation was a short *Glyceria-Festuca-Agrostis* sward beside a substream. The seedling data from this soil again show the presence of numerous seeds of *Glyceria maritima* as was in evidence in the first situation. Seedlings of *Agrostis* and *Festuca* also arose from this soil, and although there was no *Juncus maritimus* growth actually in the herbage yet this species was present on adjacent ground and the appearance of *J. maritimus* seedlings from the soil showed that it had formerly grown here, and that its buried seeds would give rise to plants should an opportunity occur.

The sward of the fourth area was composed chiefly of *Festuca* and *Agrostis* with scattered plants of *Juncus*. A considerable proportion of the ground was bare of vegetation. The seedling data are remarkable for the comparatively small number which arose from the soil. The sandy nature of this area obviously had a deterring effect upon plant growth, and therefore the quantities of buried viable seeds were few in proportion.

The fifth sampling was situated farther from the Estuary than were the foregoing, and it was bordering upon alluvial farm pastures. The sward was composed of *Glyceria maritima*, *Festuca rubra* and *Agrostis* species, but there were more miscellaneous species in evidence than in the third plant association

sampled where the main species were similar. A greater number of species of seedlings occurred in this soil than from the soils of the other areas, and evidence of the proximity of cultivation is seen in the presence of *Sagina procumbens*, *Stellaria media*, *Galeopsis Tetrahit*, *Rumex obtusifolius* and *Urtica dioica*. The large number of seedlings of *Glaux maritima* from this soil and from that of the third area is noteworthy. It is evident that large numbers of seeds of this species become buried in a viable condition, although the plants themselves may not be particularly numerous in the sward, for such was the case in both these instances.

DISCUSSION ON THE SALT-MARSH DATA

The buried viable seed data from the salt marsh shows that of the species composing the vegetation and which ripen and shed their seed comparatively few have their seeds buried in a viable condition in any appreciable quantities. The outstanding species in this respect are *Glaux maritima*, *Agrostis* species and *Glyceria maritima*. On the other hand, the small numbers of buried seeds of some of the remaining species, considering their abundance in the surface vegetation, is very marked. This is especially the case with *Aster Tripolium*, *Armeria maritima* and *Festuca rubra*. Yapp & Johns (9) have discussed the spreading capacity of the plants on the marsh, and point out that most of the grasses are stoloniferous. They further mention that the grasses do not flower freely on the closely cropped sward, but it is evident from the present data that sufficient flowering and seed setting takes place in the case of *Agrostis* and *Glyceria* to enable appreciable quantities of their seeds to enter the soil. A certain amount of spreading by vegetative means would take place among the miscellaneous herbs, particularly by *Glaux maritima* and the *Juncus* species. Yapp and Johns illustrate the erect type of growth of *Armeria maritima*. It is possible that the marked dominance of this species in the swards is chiefly caused by its shed seed giving rise to an abundant growth of seedlings. This would leave comparatively few seeds to enter the soil.

Four species mentioned by Yapp and Johns in their turf analyses of the several plant associations of the marsh did not occur in the present experiment. These were *Lepturus filiformis*, *Triglochin maritimum*, *Plantago Coronopus* and *Juncus Gerardi*. In regard to the last two species, these investigators record that they are characteristic of the higher levels. In this connexion it is significant that buried viable seeds of *Plantago* and *Juncus* species were particularly abundant in numerous soils dealt with in the previous work (1, 2). It would appear evident, therefore, that *Plantago Coronopus* and *Juncus Gerardi* were not members of the communities sampled in the present experiment.

The great abundance of *J. maritimus* on the marsh has been commented upon, and the fact can be well understood by a study of the aggressive characteristics of the plant itself. The soils sampled on the *Juncus* association were

full of the underground portions of this species, and as the data show, buried viable seeds are present to add more plants to the herbage should the opportunity occur. Even where no *J. maritimus* existed in the immediate sward, as in area 3, nevertheless the seeds were present in the soil.

The soil taken from area 1 beneath the sward next the bare silt of the river and that from area 5 on the landward side of the section investigated show interesting contrasts in their buried seed content. Only the seeds of *Glyceria maritima* occurred in both soils, whereas three other species occurred from the first situation and ten occurred from the fifth. The *Armeria-Glyceria* association forming one of the low sward zones next the river was restricted in its flora, but the sward of *Festuca*, *Agrostis* and *Glyceria* on a slightly higher level had more species in its composition of the salt marsh category and was furthermore contaminated by species from neighbouring farm land.

SUMMARY

(1) *Elevation data.* Samples of soil for their viable seed content have been taken at successive elevations on the slopes of Plynlymon and Cader Idris.

As the elevations increased so the quantities of some species became less in the surface vegetation, and their amounts of buried viable seed became correspondingly less in the soil. Other species which were abundant in the herbage throughout the slopes showed little decline in their buried seed quantities, except at the highest elevations. These differences were observed among the species of a genus as well as among unrelated species.

The limit in elevation for certain species was reached comparatively early in the series, both in regard to buried seed and surface vegetation.

Grasses were dominant in the vegetation of the majority of the areas investigated, but with the exception of *Agrostis* species the quantities of buried viable seed were not in proportion. The discrepancies in regard to the other grasses are in accordance with previous work on the subject.

There are indications that certain species rely upon vegetative means for their perpetuation, and that other species, the buried seed of which occurred in appreciable quantities at the lower elevations, rely chiefly upon vegetative means at the highest elevations investigated.

The data have given further evidence of the large amounts of buried viable seed to be found in soils of a high moisture content.

(2) *Salt-marsh data.* Samples of soil for their buried viable seed content have been examined from a section of the Dovey salt marsh.

Of the species composing the various associations, few were outstanding in having comparatively abundant viable seeds in the soils. On the other hand, the evidence indicates that vegetative means are extensively used by certain of the grasses and miscellaneous herbs for the purpose of perpetuation.

The soils underlying *Juncus* areas containing very few other species in the herbage were found to contain viable seeds of a more numerous flora.

Some species were dominant in the surface vegetation but comparatively few of their seeds occurred in the soils, while other species were opposite in this respect.

The buried viable seed data from a sward in proximity to the river was in marked contrast to that from a sward at the landward side of the section investigated.

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REFERENCES

- (1) Chippindale, H. C. & Milton, W. E. J. "On the viable seeds present in the soil beneath pastures." *This JOURN.* **22**, 508-31, 1934.
- (2) Milton, W. E. J. "The buried viable seeds of enclosed and unenclosed hill land." *Bull. Welsh Plant Breeding Station*, Series H, No. 14, 58-84, 1936.
- (3) Salter, J. H. "The altitudinal range of flowering plants and ferns in mid-Wales." *Northw. Nat.* **3**, Nos. 3 and 4, 1928.
- (4) Price Evans, E. "Cader Idris: a study of certain plant communities in south-west Merionethshire." *This JOURN.* **20**, 1-52, 1932.
- (5) Salter, J. H. *The Flowering Plants and Ferns of Cardiganshire*. The University Press Board, Cardiff, 1935.
- (6) Coulon, Jacques de. "*Nardus stricta*: Étude physiologique, anatomique et embryologique." *Mém. Soc. Vaudoise Sci. Nat.* **6**, 245-332, 1923.
- (7) Jefferies, T. A. "Ecology of the purple heath grass (*Molinia caerulea*)." *This JOURN.* **3**, 93-109, 1915.
- (8) Chippendale, H. C. & Milton, W. E. J. "Note on the occurrence of buried seeds in the soil." *J. Agric. Sci.* **22**, 451-2, 1932.
- (9) Yapp, R. H., Johns, D. & Jones, O. T. "The salt marshes of the Dovey Estuary." Part II. Yapp & Johns. "The salt marshes." *This JOURN.* **5**, 65-103, 1917.

STUDIES IN SALT-MARSH ECOLOGY

SECTIONS IV AND V

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(With ten Figures in the Text)

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IV. CHLORIDE, EXCHANGEABLE SODIUM AND CALCIUM, AND MOISTURE

Introduction

As one of the more important factors of the salt-marsh habitat, salinity has received considerable attention from various investigators. Very little, however, is known about the proportion of sodium to total chloride present in the soil or about the exchangeable calcium. It has been shown by Salisbury (1925) that the calcium content of dunes changes materially with their age, and this suggested that a similar phenomenon might be found for the soils of salt marshes. So far as British salt marshes are concerned very little quantitative data has been published for any of the above-mentioned soil constituents. Morss (1927) writing on the Merse lands of the Nith estuary concluded, from qualitative data only, that soil salinity was dependent upon

- (a) Height of the preceding tide;
- (b) Rainfall;
- (c) Height of the marshes;
- (d) Proximity of creeks and the drainage conditions;

- (e) Physical character of the mud;
- (f) Presence or absence of vegetation;
- (g) Slope of the ground;
- (h) Distance from the sea.

A detailed quantitative analysis of the salinity changes in salt pans has appeared in a paper by Nichol (1935), and therefore this aspect of the salt-marsh habitat will not be considered further here.

Theoretical considerations

It is perhaps instructive to consider what results may be expected in the case of the total chloride and exchangeable calcium of the soil in the light of the factors already studied (Chapman, 1938). A theoretical schema has been prepared (Fig. 1) to illustrate the conditions. It has not proved possible to use actual values, but the behaviour of the various factors can be regarded as approximating to the natural conditions. The depth of clay mud is shown, and on high marsh this may decrease in height near a dune system or else persist in a transition marsh (*Phragmitetum*) to a considerable depth. The height of the dominant vegetation type is also shown, and the presence of a dense algal covering, the *Pelvetia-Bostrychia* consociates and limicolous *Fucaceae* associates, in the *Asteretum* and *Salicornietum* is indicated. The marshes are drawn so as to represent increasing height with age, and so the curve for tidal inundations rises to a maximum at the lowest level. The curve for maximum non-tidal floodings behaves in a reverse manner, rising sharply to a maximum at the highest levels together with a sharp increase at the line of demarcation between upper and lower marshes as demonstrated in Paper II of this series (Chapman, 1938) (+1.3 I.Z.L.). The evaporation curve is made up of two components; (a) a component depending on the degree of exposure, and (b) a component depending on the height and density of the vegetation. The curves drawn for summer and winter attempt to present what may happen from a consideration of these two components. The amount of rainfall over the marsh is largely constant with perhaps a slight decrease on the low marshes to allow for rain that falls when the marshes are flooded. From a consideration of these factors we may try to anticipate the behaviour of the total chloride and exchangeable calcium in the surface layers at the different marsh levels.

Bare sand flat—lowest marsh. During the winter, spring, and autumn the total chloride will probably be maintained at a value near that of sea water because of the constant flooding. In summer, however, the rapid run off of the water, coupled with exposure to much evaporation because there is no vegetation to impede it, may be expected to raise the total chloride concentration. The exchangeable calcium should be high, as there is little leaching and the sand is largely virgin.

Salicornietum. The total chloride concentration will probably be just below that of sea water, but will not rise much in summer because of the vegetation,

including the algal mat of *Fucus vesiculosus* ecad *caespitosus*, which must lower evaporation. The exchangeable calcium should be high because relatively little leaching has occurred, and also the soil contains numerous empty shells of the mollusc *Hydrobia ulvae*.

Asteretum. The total chloride may be expected to behave as in the *Salicornietum* and for the same reasons, except that the algal vegetation is a dense mat of *Pelvetia canaliculata* forma *libera* and *Bostrychia scorpioides*. In the clay surface mud, resistance to water flow is great and much of the moisture is retained, and this will also tend to keep the chloride concentration low. The exchangeable calcium will be high as in the *Salicornietum*. The presence of creeks here and in the *Salicornietum* should keep the chloride content of the adjoining marsh near that of sea water because of the continual tidal influence.

General salt marsh (G.S.M.). This community occurs on upper marshes only and hence, whilst in winter the total chloride may be somewhat below that of sea water because of the relatively fewer submergences, nevertheless in summer it may rise considerably because of the long periods during which no tide covers the marsh, and during this exposure the low habit of the vegetation should not greatly impede evaporation. In all the communities the surface mud layer has a high resistance to water flow, and when evaporation takes place from the surface it is doubtful how far the water lost is replaced at a commensurate rate, and this water deficiency may consequently cause the chloride concentration to rise. The exchangeable calcium will be lower because of the longer time during which leaching can have taken place.

Plantaginetum. As for the G.S.M. In both these communities the presence of creeks may be expected to lower on the adjoining marsh the values in summer, and in winter to raise the lowered values towards that of normal sea water.

Juncetum—highest marsh. There is very little tidal flooding so that the influx of salt is not great, and the height of the vegetation may also lower evaporation so that the total chloride content on these grounds should be low. The exchangeable calcium should also be low unless there is a neighbouring dune system when blown sand will tend to raise it.

Phragmitetum. The total chloride will be very low because tidal flooding is rare, there is usually some fresh water draining in, and the height of the vegetation may lower the degree of evaporation. In both this community and the *Juncetum* the presence of creeks should raise the chloride content of neighbouring areas to some degree.

We may therefore expect a whole complex of factors to be operating at any one given level so far as the surface layer is concerned. The total chloride of the lower layers should get less and less with increasing marsh height and the concomitant decreased number of inundations. This, however, may be counteracted near creeks where regular seepage will raise the total chloride concentration towards that of sea water.

Technique

During the summer of 1935 a series of observations were made upon the total chloride content of the soil in four different plant communities at three levels, the surface, 3 in., and 9 in. In addition, a number of random samples were collected from several other plant communities on different Norfolk marshes.¹ From May 1937 to April 1938, a monthly series of estimations was made on samples taken at the surface, 3 in., and 9 in. from a *Salicornietum*, *Asteretum*, general salt marsh (G.S.M.), and *Juncetum maritimae* on Scolt Head Island. The total chloride, the exchangeable sodium, and exchangeable calcium were estimated in all these samples. The moisture content of every sample was determined on the fresh-weight basis as soon as possible after collection because the results are all expressed as percentages of the moisture content. An essential preliminary to an investigation of this nature was to determine the sampling error. As a result of some initial analyses it was concluded that at least five samples must be taken at each depth (Chapman, 1936). In 1935 the samples were analysed in the field laboratory at Brancaster Staithe and so the water content was determined by putting small portions in specimen tubes and heating them in a hot kitchen oven for 36 hours. This technique appeared to be entirely successful. The later samples employed for the moisture determinations were all dried in an electric oven at 105° C. The chemical estimations were carried out on air-dry samples, using the following methods.

Total chloride. During 1935 and 1937 the following technique described by Adriani (1934) was employed. Ten grams of dry soil were taken and leached with occasional shaking for 24 hr. in a flask with 100 c.c. of 1 % sodium sulphate solution, which facilitates subsequent filtration. The solution was then filtered off and in the later part of 1937 and also in 1938 washed with 50 c.c. of distilled water yielding a solution containing 1 g. of dry soil in every 15 c.c. solution. Prior to 1938, 50 c.c. of the 100 c.c. filtrate were removed and the soil washed with a further 50 c.c. of distilled water, thus yielding a solution containing 1 g. of soil in every 20 c.c. solution. This earlier method tended to give values very slightly lower than those obtained during 1937-8, but they do not materially invalidate the general conclusions. In 1935 and the earlier part of 1937, 10 c.c. of the filtered solution (1 g. per 15 c.c.) were removed and titrated with standard silver nitrate solution such that 1 c.c. standard solution was equivalent to 0.001 g. chlorine. In 1937 this means of estimation was abandoned in favour of a more sensitive titration technique with the standard silver nitrate whereby the end-point is determined electrically (Wright, 1934). The chloride content was then calculated as a percentage of the water content because it is the concentration in the soil solution that we may expect to affect the distribution of the plants.

¹ In a *Juncetum* and *Phragmitetum* the lowest samples were collected at one foot.

Exchangeable sodium. The uranyl zinc acetate method was employed for these determinations. Two grams of dry soil were taken and leached overnight with 80 c.c. of $N/5$ acetic acid. The solution was then filtered off and 40 c.c. removed for the sodium estimation and the remainder used for the CaO analysis (see below). The 40 c.c. of solution were evaporated to dryness, taken up in about 1 c.c. aqua regia, and transferred to a crucible and the evaporating basin washed out with another 1 c.c. of aqua regia. The contents of the crucible were evaporated carefully to dryness and the crucible then heated at a red heat for 2 hrs. When cool 10 c.c. of water were added, the sides of the crucible thoroughly scraped, and the water extract filtered to remove sediment. One c.c. of the filtered extract was taken and put in a small porcelain dish with 10 c.c. of the zinc uranyl acetate solution made up according to directions (Steiner, 1934). This mixture was allowed to stand for 48 hr., when the sodium crystals were filtered off through a Gooch crucible lined with two circles of filter paper, and washed several times (a) with more zinc uranyl acetate, (b) 95 % alcohol, and (c) ether. The crucible was then allowed to stand 7–10 min. before weighing. The weight of the precipitated sodium salt multiplied by the factor 0.1495 gives the weight of exchangeable sodium contained in 1 g. of the dry soil.

Exchangeable calcium. To the surplus solution left after removal of the sodium sample a drop of ammonia was added together with a small quantity of solid ammonium chloride and then excess of a strong solution of ammonium oxalate. The precipitate of calcium oxalate after standing overnight was filtered off, washed with warm water, and dissolved up whilst still on the filter paper with a dilute solution of sulphuric acid. The resulting solution was titrated with $N/10$ potassium permanganate and the exchangeable calcium (CaO) expressed as a percentage of the water content.

Results. In the course of this study considerable data have been accumulated and it has not always proved possible to exhibit it in graphic form without increasing the number of figures unduly. In such cases representative graphs have been selected, but the discussion is based upon a consideration of the whole series of graphs. In order to conserve space it has also been necessary to refrain from publishing the graphic results for 1935, but these results have been considered in the text. It has already been mentioned that in order to eliminate any sampling error five samples were collected and analysed from every site, and so the results have been expressed graphically in bands rather than in single line curves, the width of the band representing the range of variation found on any given date.

A. Total chloride content

Annual drift (Fig. 2). Two important facts emerge from a study of the curves for the surface layers. The first is the low values recorded in January and to a lesser extent in February. In 1937 the winter was mild, and germina-

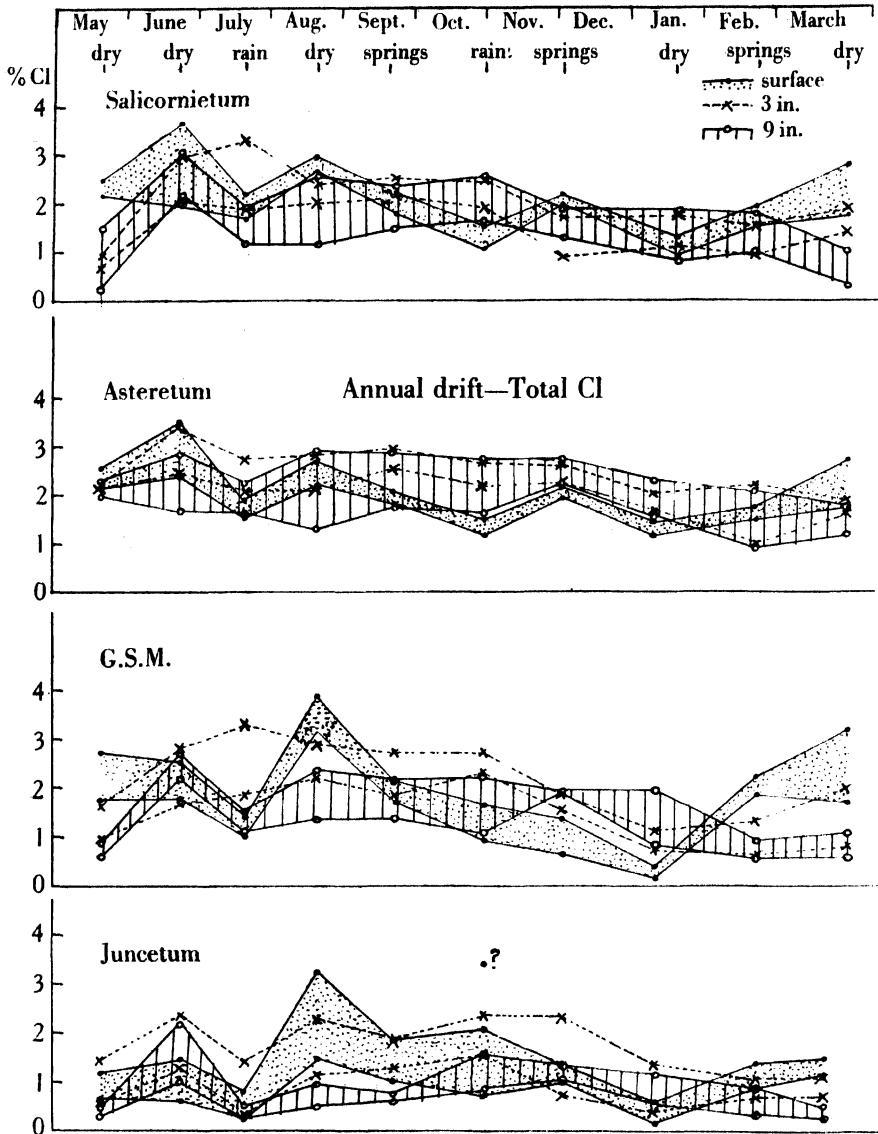


FIG. 2. Annual drift of the total chloride in four marsh communities.

tion of many of the seeds probably took place during this period. A similar spring fall in the surface total chloride has been recorded from American salt marshes, and it is therefore suggested that these low spring values enable germination of the seeds to take place.¹ This is particularly important on the

¹ Experimental evidence has been accumulated which shows that most salt-marsh species only germinate under conditions of low salinity.

higher marshes where the total chloride content may attain to much greater values later on in the year. The second significant feature is the influence of rainfall upon the surface chloride, as shown by a drop in all the curves for October and July (Fig. 2). As may perhaps be expected, the values obtained during spring tidal periods are lower than those obtained during neap tides, because the absence of tidal flooding in the summer enables evaporation to proceed to such a degree that the total chloride concentration is materially increased. The highest values are recorded from the G.S.M. and Plantaginietum during the summer months. These high values can probably be correlated with the low growth habit of the vegetation, because on the higher marshes the habit of the dominant species, *Juncus maritimus*, should tend to prevent evaporation, whilst on the lower marshes the more frequent tidal inundations keep the chloride concentration steady. It is also of interest to note that the algal species which occur in the G.S.M. and Plantaginietum are few in number (two Chlorophyceae, two Phaeophyceae, and some Cyanophyceae), and these reach their maximum abundance in winter when the surface chloride values are at their lowest. It is the author's opinion that on the lower marshes (Salicornietum and Asteretum) the chloride content of the surface layers is controlled primarily by the operation of the tides and the incidence of rainfall, whilst on the higher marshes the character of the vegetation must also be considered as an important factor, especially during the summer months (cf. p. 175).

The curves for the 3 in. layers of the different communities have a tendency to be high in the late summer and autumn and to fall in the winter and early spring. The roots of many of the plants are in this layer, and it is possible that the high autumn values bring about the termination of the active growth period for some species, whilst new growth is initiated during the period of the lower spring values. It has been demonstrated, for example, that the osmotic pressure of *Juncus maritimus* rises steadily until the end of the growing season (Schratz, 1934). The content of the 9 in. layer does not exhibit any fluctuations which can be correlated directly with seasonal or other factors.

Horizontal variations (Fig. 3). Here it is of extreme interest to determine whether there is any constant significant variation between the different communities because previous authors have suggested that variations in salinity are largely responsible for the zoning of the halophytic vegetation. The results obtained indicate clearly that there is no essential variation between any of the soil layers in the Salicornietum and Asteretum. There is, however, a regular fall in the average values for all three soil layers from the Asteretum to the Juncetum (cf. Table I), so that if the total chloride content controls the occurrence of the vegetation zones it can only be so on the higher marshes. The mere fact that the average values of all the samples taken throughout the year may exhibit a gradient from the Asteretum to the Juncetum does not mean that the values for any one of the monthly samplings will do likewise. So far as the maximum values which were recorded during the year are concerned, there

would appear to be no gradient except in the 9 in. layer, and even here it is only in the Juncetum that there is a relatively low value (cf. Table I). In other words, the roots of the plants must be able to tolerate a high chloride value for a short period in any of the communities, irrespective of marsh height. It may

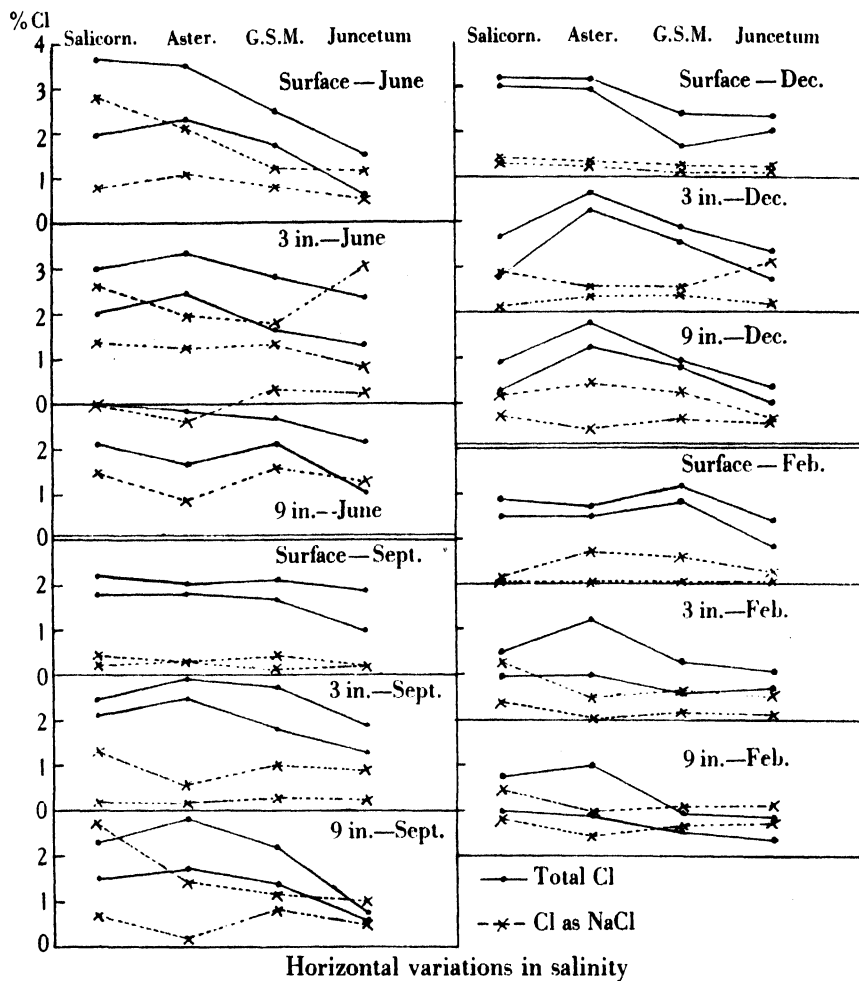


FIG. 3.

Table I. Chloride as percentage of water content. Average and maximum values of 50 samples in each community collected in 10 monthly sets of 5 samples each

Community	Average value			Maximum value recorded		
	Surface	3 in.	9 in.	Surface	3 in.	9 in.
Salicornietum	2.0	2.0	1.75	3.5	3.25	3.0
Asteretum	2.0	2.25	2.0	3.5	3.3	2.9
G.S.M.	1.8	1.8	1.5	3.75	3.3	2.5
Juncetum	1.25	1.3	0.8	3.25	2.3	2.15

be that the vegetation is determined to some extent by the periodicity of these maximum values, particularly in summer, but there are no data available to show the length of time they may persist.

Vertical variations. The only useful information that emerges, and that rather of a negative character, is the lack of regularity from month to month. In all the communities there is usually a fall from the 3 to the 9 in. layer, whilst the gradient between the surface and 3 in. layer may be of any nature. The Juncetum is the only community in which a marked increase in concentration of total chloride with increasing depth can be noted at any time during the year (Fig. 2, June and October to January). The gradients for the Asteretum and Juncetum were similar in the summers of 1935 and 1937, but the gradients for the G.S.M. in July of these two years are very different. This can perhaps be accounted for by differences in the climate of the two years at the sampling period together with the low habit of the vegetation which allows full scope for the climatic and tidal factors to operate. In the Asteretum the nature of the phanerogamic vegetation itself must lower surface evaporation, whilst the presence of a dense algal community of *Pelvetia canaliculata* ecad *libera* and *Bostrychia scorpioides* effectively prevents any little evaporation that might be permitted among the *Aster* plants (cf. p. 173).

B. *Exchangeable sodium, expressed as equivalent chloride*

Annual drift (Fig. 2 *a*, which should be compared with Fig. 2 as the estimations are all based on the same samples). The most important feature here is the fact that the exchangeable sodium accounts for only a small fraction of the total chloride content of the surface and 3 in. layers, whilst it frequently more than accounts for the total chloride of the 9 in. layer. Various explanations of this phenomenon would appear to be possible. Leaching may bring about an accumulation of other sodium salts in the lower layers: alternatively, much of the sodium may not be present in an exchangeable form and hence cannot be extracted by the usual means. It also opens up the problem as to how far the sodium chloride present in the soil is dissociated, especially in the upper layers, and if it is so, whether the sodium ion is more closely bound to the colloidal soil particles. It can be noticed that the high exchangeable sodium is associated with the sandy layers, whereas it is low in the mud layers where the soil is colloidal. It is also possible that there is an unequal absorption of the two ions by the roots of the plants. This aspect of the problem is being subjected to further study. Furthermore, there may be an abundance of chlorides other than that of sodium in the surface layers of the soil but hardly to the extent required by the figures. Without further study it would be profitless to discuss here the relative merits of these various hypotheses. One other point that may be commented upon is that the sodium content does not follow the same annual drift as the total chloride because, whereas the latter in the surface layers fell to a minimum in January in all the communities, the

sodium exhibited very little fluctuation throughout the year in any of the layers in the different communities. Likewise, the effect of rain upon the chloride content of the surface layers is not reflected in the sodium content. This suggests that the sodium in the soil is present in at least two states, only one of which, the bound sodium, is influenced by season and rainfall.

Horizontal variations (Fig. 3, "NaCl" curve). Here again there is no apparent correlation between the total chloride and exchangeable sodium because they may frequently change in quite opposite directions. On the whole there is a slight tendency for the exchangeable sodium to decrease with increasing height of the marsh above sea-level.

Vertical variations. The dissimilarity between the behaviour of the sodium and chloride curves is most pronounced because of the high sodium values in the 9 in. layers. For this reason the sodium gradient in all the communities is frequently the reverse of the chloride gradient and rises with increasing depth. This dissimilarity between the exchangeable sodium and total chloride opens up a problem which requires further investigation. The greater proportion of exchangeable sodium in the more sandy layers, e.g. 9 in. layers in all communities and 3 in. layers in *Salicornietum* and *Juncetum*, strongly supports the thesis of absorption of sodium ions in the clay layers.

C. *Exchangeable calcium*

Annual drift (Fig. 4). There does not appear to be any significant variation that can be correlated with either the tidal phenomena or with rainfall. Such variations as do occur must be caused by other, as yet, unknown factors.

Horizontal variations (Fig. 5). In general the exchangeable calcium of the surface layers reaches a maximum in either the *Salicornietum* or *Asteretum*. These maxima can be attributed partly to lack of leaching and partly to the abundance of shells of *Hydrobia ulvae*, a small mollusc which is very prolific in both communities. This provides an example of an animal influencing one of the soil factors to a marked degree. In the 9 in. layer the outstanding feature is the very high content found in the *Salicornietum*, up to 28 % in one case. The reason for this is somewhat obscure but may be connected with the proximity of young dunes which likewise should have a high content (Salisbury, 1925). Whilst there is a gradient in the 9 in. layer from the *Salicornietum* to the G.S.M. a slight increase may occur between the G.S.M. and *Juncetum*. This can also be explained by the proximity of dunes because Station 3 in the *Juncus* was at the base of a dune system. Fig. 4 gives all the values obtained during one year for the different marshes, and it can be seen at once that there is in general a gradient in the various layers which may be correlated with increasing marsh height—and hence age. The curves are very akin to those found by Salisbury (1925) for the dunes at Blakeney. Stations which are sandy in nature, *Salicornietum* 3 and 9 in., *Asteretum* and *Juncetum* 9 in., tend to show

the highest values and also the greatest variation. This may be a further phase of the distinction between the clay and sandy soils.

Vertical variations. The effect of leaching by the tides and rainfall generally results in an increasing calcium content with increasing depth. This forms the

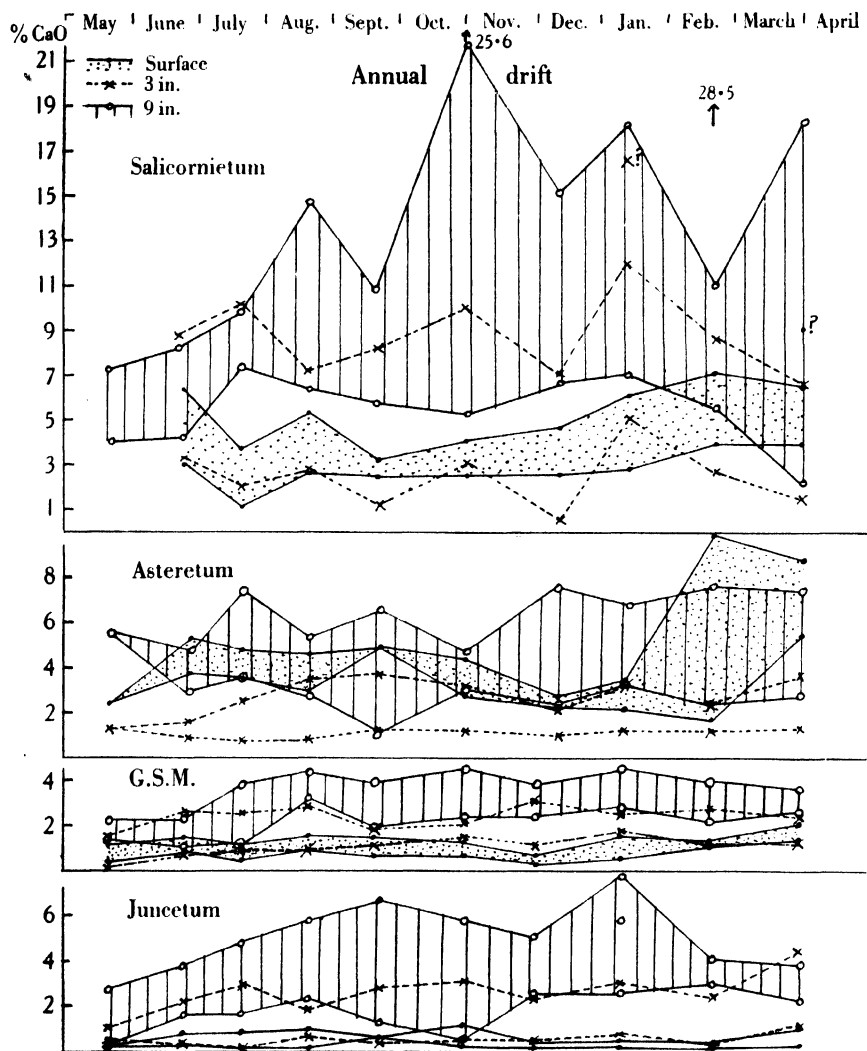


FIG. 4. Annual drift of exchangeable calcium in four marsh communities.

normal gradient for the G.S.M. and Juncetum throughout the year but in the Salicornietum and Asteretum it is replaced at times by a gradient having the minimum value at the 3 in. level. In the former community the relatively thin mud layer and proximity of dunes is probably the explanation, whilst in the latter the presence of the *Hydrobia* shells raises the surface values.

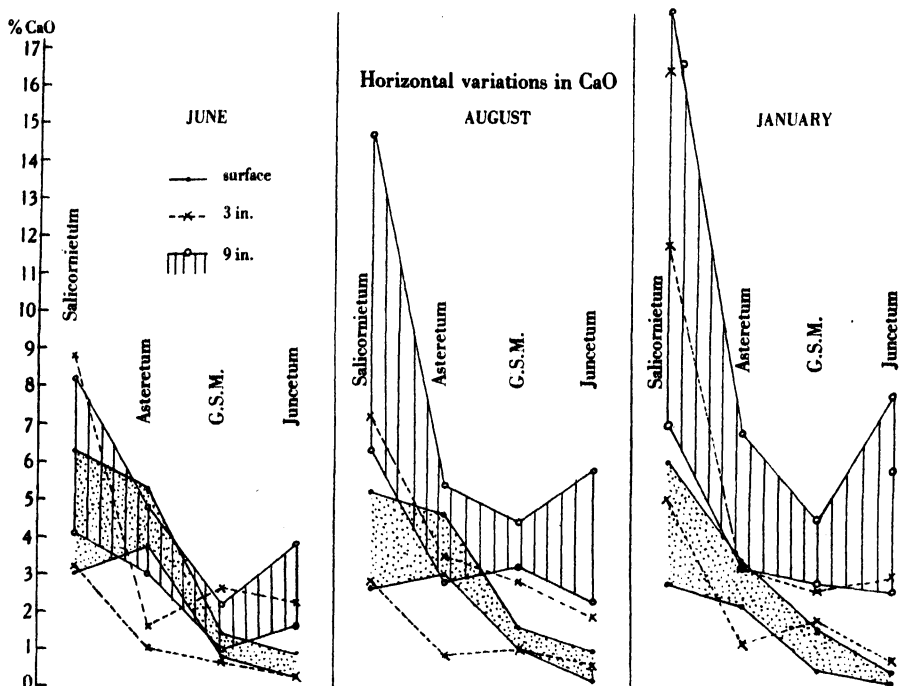


Fig. 5. Horizontal variations in exchangeable calcium.

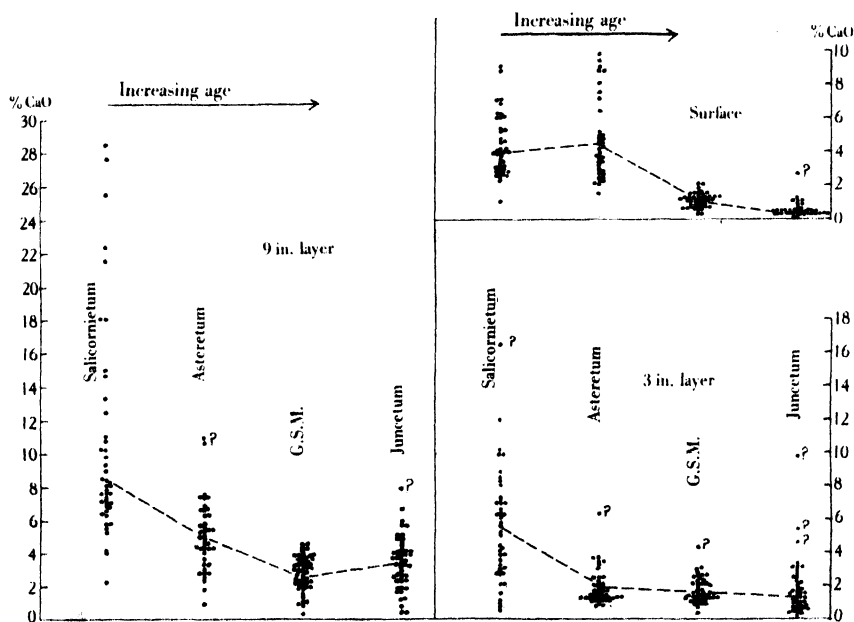


FIG. 6. Horizontal variations of CaO throughout one year in relation to age of marsh.

D. *Total chloride content and communities of the prisere* (Fig. 7)

A study of other salt-marsh communities brings out certain features which can perhaps be best illustrated by considering the chloride values for different marshes in midwinter and midsummer. In the latter season it is found that there is a definite sequence of events as the marshes increase in height. This sequence was established through measurements made in 1935 and also in 1937-8. In the summer the chloride content in the surface layers of the bare sand or mud flats is extremely high, up to 16 %. At 3 in. depth, however,

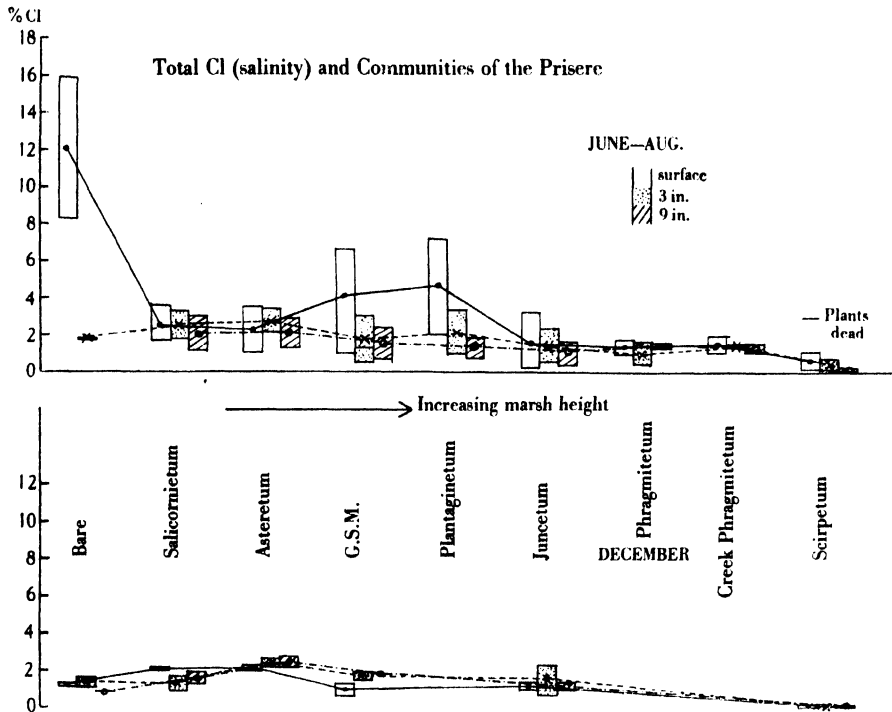


FIG. 7.

evaporation does not exert such an influence and the total chloride is only about 2 %. In the *Salicornietum* the surface value rarely reaches 4 %, whilst that of the *Asteretum* is either the same or somewhat lower. Then, with increasing height, in the *G.S.M.* the values in the summer for the surface layers may attain to 6 % Cl depending upon the heat of the summer and the conditions under which the samples are collected, whilst maximum values were recorded from the *Plantaginetum* with 7 % Cl. Rainfall has a marked temporary effect by depressing the surface values for a day or two. The size and period of this effect depends on the amount of rainfall. The total chloride is also much influenced by the type of summer, whether hot or cool.

Still higher marsh bearing a *Juncus* vegetation has a relatively low chloride value in the surface layers (about 2 %). Where there is active *Phragmites* invasion it is found that along creeks the surface layers have a chloride value just below 2 %, whilst farther away from the creeks the value is nearer 1 %. The higher creek values must be caused by the relatively easier access of sea water not only through flooding but also by lateral seepage (Chapman, 1938 and also p. 163). In a *Scirpetum* the values in the surface layers rarely rise above 1 % and most usually are about 0.5 %. In the 3 and 9 in. layers there is considerably less fluctuation between the different communities and very little to which any significance can be attached. The highest values commonly occur in the lowest marshes when the sand substrate permits the sea water to penetrate more readily. In the older marshes the depth of mud is much greater and the movement of water much less (Chapman, 1938). It would seem clear that very few plants could tolerate the high values reached by the surface layers of the bare sand flats in summer, and experiments tend to show that *Salicornia* is probably the only species that can. Any other plants that may germinate on the sand and mud flats in the spring when the chloride content is low would be killed by the high summer increase unless their roots had been able to penetrate quickly into the lower layers. This factor excludes from such areas slow-growing plants like *Limonium vulgare*, *Armeria maritima*, *Triglochin maritimum*, *Spergularia marginata* and *Plantago maritima*. The advent of *Salicornia* spp. brings about an increased deposition of mud, and water is retained to a much greater extent by the fine silt than by the coarse sand (Chapman, 1938, and section on moisture). With the higher water content of the mud in the *Salicornietum* the total chloride is considerably reduced in relation to the bare sand flats even in the summer, and it may be this summer reduction which makes it possible for the next species—*Aster*—to enter the area. The colonization by *Salicornia* and its successful establishment brings about a new set of conditions whereby another plant can invade the area successfully. It is, of course, also possible that the *Salicornia* plants actively remove salt from the soil in considerable quantity. This is a problem which it is hoped to study further. The next change serves to bring out clearly one of the great differences between the upper and lower marshes. In the G.S.M. and *Plantaginetum* the surface layers may attain to a high chloride concentration in the summer—up to 7 %. This can be explained on the bases set out on p. 163.

(a) Long periods of non-tidal flooding with consequent evaporation all the time.

(b) A clay soil in which water is removed from near the surface, but the high resistance prevents more capillary water from below replacing the water lost sufficiently rapidly to keep the chloride concentration low.

(c) A vegetation life form which is conducive to much evaporation because the plants are all small, rarely exceeding 6 in. in height. The only exceptions to this are areas where *Glyceria* (*Puccinellia*) is dominant, and, if not grazed, the

ground in such a place irrespective of marsh height is always much moister than elsewhere and the chloride concentration must be correspondingly lower.

The lower marshes, with their more frequent flooding during the summer months, never reach the high chloride values of the upper marshes. This is probably the explanation of the distribution of many of the algae—especially the Chlorophyceae. The bulk of the algae on the upper marshes are gelatinous forms such as *Rivularia*, or sheathed forms such as *Lyngbya* and *Microcoleus*, and these protective coverings probably enable them to survive. The fact that the plants in the G.S.M. and Plantaginetum are able to exist must be because their roots in the 3 and 9 in. layers do not have to tolerate such high salinities. It is perhaps worthy of comment to note that very few of the salt-marsh species are annuals, and this may be one reason why the vegetation can persist on the marshes at such a time, because the species are well established by virtue of their underground rhizomes. The only common annuals—*Salicornia* spp. and *Suaeda maritima* var. *flexilis*—appear capable of tolerating relatively high chloride values. It is, moreover, of common occurrence to see salt crystals on the leaves of *Limonium vulgare*, *Plantago maritima*, and *Armeria maritima*, and so it must be assumed that their internal economy must be capable of withstanding great changes.

The chloride values in the surface layers fall again in the next highest marsh community—the Juncetum. This fall in value can be ascribed to the height of the marsh and the nature of the dominant species, *Juncus maritimus*. The tall leaves and flowering scapes act as a blanket, and evaporation must be slow as compared with the Plantaginetum. This fact probably explains the presence of the occasional *Aster* plants that may be found in the Juncetum, although they are absent from the G.S.M. and Plantaginetum. *Aster tripolium* would probably extend over a considerable vertical range were it not for the high chloride concentration young plants would have to face in the summer. As a result the vertical distribution is discontinuous, the species being absent from the G.S.M. and Plantaginetum and appearing again in the Juncetum and Phragmitetum. A similar explanation will account for the frequent occurrence of *Aster* in parts of an Obionetum. Another feature of the Juncetum is the richer growth of the accompanying plants. *Limonium vulgare* may attain to a very large size when it grades into var. *pyramidalis* which probably should be regarded as a phenotype. Observations in the field and from culture experiments show that high chloride values have a stunting effect on most species and the plants of the G.S.M. and Plantaginetum are never very large, whereas the same species occurring in the Juncetum are usually much more luxuriant in their growth.

On the mainland marshes where the Juncetum grades into a Phragmitetum there may be a further slight drop in the chloride value of the surface layers, but that of the lower layers does not materially alter. The lower surface values are probably produced by (a) even less tidal flooding, (b) still less evaporation

because of the dense tall plants, (c) traces of fresh water coming from upland streams and springs. Associated plants such as *Obione*, *Aster*, and *Triglochin* are always larger, but they rarely produce flowers because of the low light intensity. Where *Phragmites* occurs along a creek the chloride values at all depths tend to be somewhat higher than in areas farther away. The *Phragmitetum* grows in a silty soil and hence sea water will only penetrate a short distance from the creek by seepage, and it is this lateral penetration which raises the chloride values in the creek community. A *Scirpetum* is usually only to be found where the total chloride is 0.5 % or lower, and so it may be concluded that neither *Scirpus maritimus* nor *S. Tabernaemontani* can tolerate a high chloride content.

If a study is made of the same marshes in the winter it will be found that the surface layers of all the communities have low values, even the bare sand flats, and that there is very little fluctuation between the chloride contents of the different layers in traversing the marshes from a *Salicornietum* to a *Juncetum*. The *Scirpetum*, and probably also the *Phragmitetum*, have somewhat lower values, but that is again because they probably cannot tolerate too high a chloride concentration. The extent of their invasion of a salt marsh on a stable coastline must be determined very strictly by the chloride content of the soil. So long as the invasion is purely vegetative, as seems to be the case with *Phragmites*, the presence of the plant must bring about a change to conditions which are more favourable to its survival. A comparison of the graphs for winter and summer (Fig. 9) emphasizes the fact that so far as total chloride is concerned there is little or no difference between the upper and lower marshes in winter, but that there is a big difference in summer which may be of fundamental importance to at least some of the species. One further small feature is the greater range of the chloride content in the different layers that is to be found in the marshes in summer as compared with the same marshes in winter. A possible explanation is that local conditions have a much greater effect on evaporation and consequent chloride concentration in the summer than in winter.

E. Moisture (expressed as a percentage of the fresh weight of soil)

The factors which influence the moisture content of the marsh soils are not so numerous as those which appear to determine the salinity. They are briefly:

(a) *Height of marsh*. This factor controls the number of tidal submergences, and although its effect is not very pronounced nevertheless it is clearly present, e.g. the September records in the curves for the *Salicornietum* and G.S.M.

(b) *Phanerogamic vegetation*. This plays an important part in controlling the evaporation from the soil; the moisture content of the surface layers in communities such as the *Juncetum*, *Phragmitetum*, and *Scirpetum* is always much higher than in any other salt-marsh community. The effect of the vegetation

can, however, be counteracted by the operation of either of the two following factors.

(c) *Proximity to creeks, and hence the influence of drainage.* This factor, as will be shown later for the *Phragmitetum*, may have the effect of lowering the moisture values at all depths.

(d) *Geological composition of the marsh.* This is of prime importance, and the data can be readily understood in most cases if the physical character of the soil is known. The water content of sand is always very low, whilst that of a clay silt is always relatively high. This is due to the differences in soil resistance and their bearing on drainage. A coarse silt is intermediate whilst a peaty soil may have a fairly high moisture content. The relation between soil moisture and soil type is very close even though a similar close relationship between salinity and soil type does not appear to exist.

Annual variation (Fig. 8). There is no significant annual variation in the different layers of any of the communities studied in detail. This is a marked contrast to the behaviour of the salinity content which exhibited distinct seasonal fluctuations. Rainfall and the incidence of spring tides do not appear to be significant factors, although the tidal factor may occasionally raise the moisture content of the 9 in. layer (e.g. *Asteretum*).

Horizontal variation (Fig. 8). There is a marked gradient here which can be correlated with increasing marsh height. The moisture content of the surface layers increases with increasing height of marsh and reaches a maximum in the *Phragmitetum* and *Scirpetum*. In the monthly series the surface of the *Juncetum* always yielded the highest moisture content. This increasing moisture content is probably due to the greater accumulation of fine silt with the developing age and height of the marsh. A type of vegetation which prevents excessive evaporation will also be a contributory factor. There does not appear to be any significant gradient in the 3 and 9 in. layers with increasing marsh age. The effect of soil type was obvious in the 9 in. layer of the *Asteretum* where the clay layer extended below the 9 in. in sites A_4 and A_5 , and these two stations always yielded much higher values than sites A_1 – A_3 which were pure sand at 9 in. This difference in soil character accounts for the wide band in the *Asteretum* 9 in. layer (Fig. 8), because normally there is very little variation between samples at 9 in., and also for the upward rise in the curves at the *Asteretum* phase in passing from the *Salicornietum* to the G.S.M.

Vertical variation (Fig. 8). The characteristic feature here is the regular decrease in the moisture content with increasing soil depth. This is to be associated with the increasing percentage of sand at the lower depths and the consequent improved drainage. The gradient is greatest in those communities where the change of soil type is most pronounced, e.g. G.S.M. and *Juncetum*, and least where there is little or no change in the soil, e.g. *Phragmitetum* and *Scirpetum*. The same feature would exist to an even more marked extent if the results were expressed as a percentage of the dry soil, but a different picture

might be obtained if a volume basis were employed. It would seem desirable that the method of expressing moisture content should be re-examined.

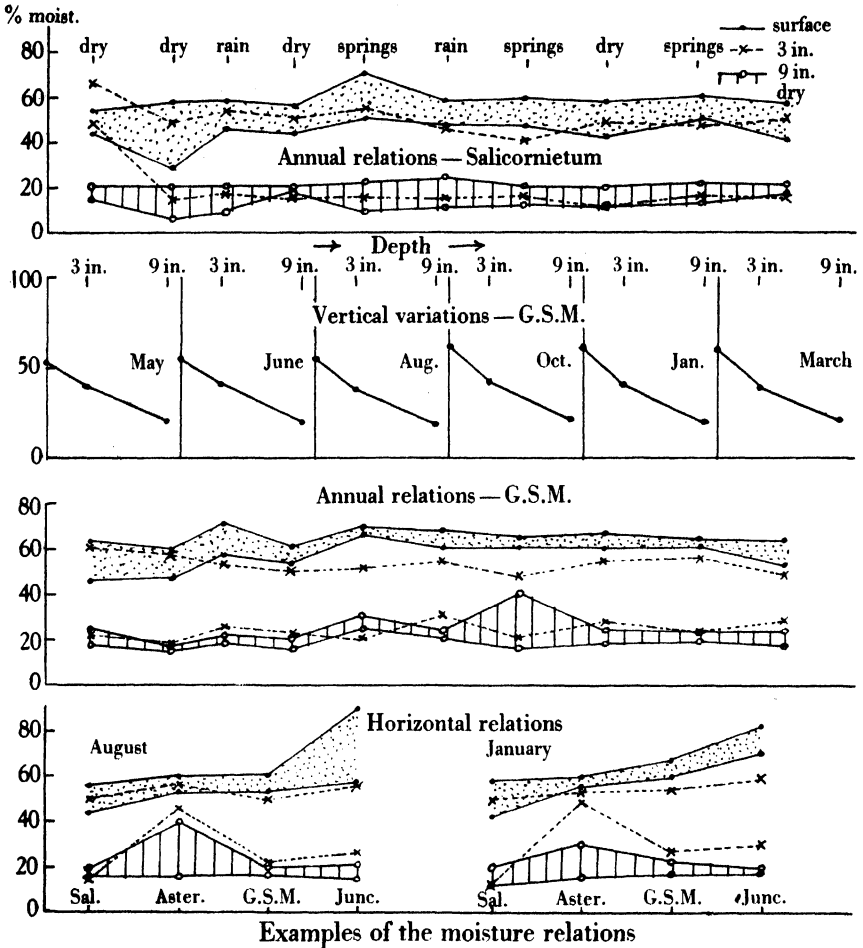


FIG. 8.

F. *Moisture in the communities of the prsere* (Fig. 9)

It can be seen at once that there is no distinction between upper and lower marshes comparable to that found in the summer months for total chloride. The most significant feature is the gradual rise in the surface moisture content with increasing marsh height. It has been suggested earlier that the greater proportion of silt on the higher marshes may account for this phenomenon. The 3 in. layer in the Asteretum has a higher average value than the corresponding layer in the G.S.M., and this can be explained by the greater proportion of sand in the G.S.M. from which the samples were taken as compared with the clay mud of the Asteretum. The consistently low values for the 9 in. layers

of all communities up to the Juncetum, except for the two stations in the Asteretum, are due to the sandy nature of the soil at that depth. In the Phragmitetum and Scirpetum the clay soil descends to a depth greater than 9 in. and hence all the samples were of a "clayey" nature. As a result there is very little difference in the average moisture contents at the different depths, and they are all very high when compared with those from similar layers in the

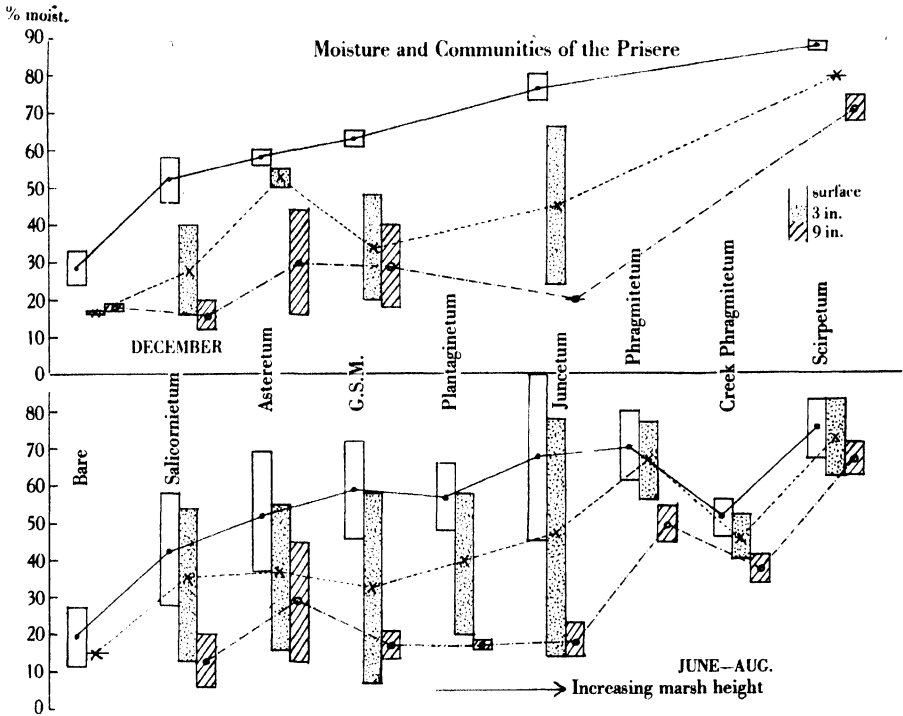


FIG. 9.

lower marshes. The figures obtained from the Phragmitetum bordering a creek make the effect of improved drainage upon the moisture content clearly evident.

Conclusions

1. The total chloride content in the different layers of the Salicornietum, Asteretum, G.S.M., and Juncetum fall to a minimum in early spring, and are therefore low at a time when seed germination may be expected to commence. It is suggested that this early spring fall in the surface layers enables the seeds of several species to germinate when otherwise they could not. If in any year this lowering fails to occur it may be anticipated that percentage germination of many species in that year will be low.

2. Rainfall acts as a distinct depressor upon the surface chloride concentration, especially in the summer months but rather less so in the winter months.

3. There is no distinct permanent gradient between the *Salicornietum* and *Asteretum*, but there is a tendency for the gradients at the various levels to fall with increasing height of marsh above the *Aster* stage.

4. There is a considerable fluctuation in the chloride content of the different layers of the various communities throughout the year, but the maximum values recorded from the different layers for the four communities studied in detail are about the same. This must mean that *maximum* chloride concentration is *not* one of the primary factors determining zonation on salt marshes at these particular levels. On the other hand, the average total chloride concentration throughout the year may be more important in this respect.

5. In so far as salinity of the surface layers is concerned there is a marked contrast in the behaviour of the upper and lower marshes in the summer months when the chloride content of the G.S.M. and *Plantaginietum* may rise to 6 or 7 %. The high summer values in the surface layers may be lowered temporarily by rainfall.

6. Bare soil attains extremely high values in the surface layers during the summer, and this factor probably prevents many species from entering such ground as colonists. *Salicornia* spp. would appear to be the only species capable of so doing.

7. The relationships that may be expected between marsh height, tidal submergence, soil structure, vegetation, drainage and the total chloride concentration appear to be fulfilled in these marshes. The total chloride, exchangeable sodium and calcium can only be satisfactorily explained by the interaction of a complex of the above factors.

8. The exchangeable sodium when studied in detail does not account for the total chloride content of the soil except in the 9 in. layers where it is present in more than sufficient quantity. This fact could be explained by one of the various hypotheses which were suggested. A fact to be considered in this connexion is the association of low exchangeable sodium values with the clay layers.

9. The exchangeable sodium exhibits no significant annual drift nor does it appear to be influenced by rainfall.

10. The exchangeable calcium tends to reach a maximum either horizontally or vertically when one or more of the following factors are operative:

(a) Proximity of dunes.

(b) Effect of leaching.

(c) The presence of numerous shells of *Hydrobia ulvae*.

11. Moisture is not a significant factor directly but it may operate indirectly. The vertical gradient decreases with increasing soil depth.

12. The principal factors which account for the phenomena associated with moisture content are:

(a) Geological composition, e.g. whether sand, shingle, mud, or peat.

(b) Nature of the vegetation in relation to surface evaporation.

(c) Proximity of creeks and concomitant drainage.

Surveying the factors postulated by Morss as controlling salinity, it may be concluded that so far as the Norfolk marshes are concerned drainage, slope of ground, and distance from the sea do not appear to be operative factors. On the other hand, rainfall, presence or absence of vegetation and especially type of vegetation, tides, height of marshes—whether upper or lower marshes—and the physical character of the soil in relation to evaporation are all factors of importance, the dominant factor in any one locality probably being dependent upon local conditions. To the factors postulated by Morss one more may now be added, namely, the proximity of fresh water from the uplands, as seen in Norfolk at Brancaster and Thornham where transitional stages to fen can be observed.

V. THE VEGETATION

Introduction

In the preceding section and in an earlier communication (Chapman, 1938) an attempt has been made to give a fairly complete description of the purely physical characteristics of Norfolk salt marshes. The present section contains a description of the vegetation of the marshes, whilst in a later communication an attempt will be made to correlate the known physical factors with the distribution of the different species.

The phanerogamic vegetation

This has already been described in some detail in the handbook (Chapman, 1934), and hence need not be repeated here. On the mainland marshes where there is an influx of fresh water the Juncetum is replaced by a Phragmitetum, in which *Scirpus Tabernaemontani* and *S. maritimus* may be locally sub-dominant. In addition to these plants the Phragmitetum may also contain *Limonium vulgare*, *Obione portulacoides* var. *latifolia*, *Aster tripolium*, *Glaux maritima*, *Triglochin maritimum*, *Juncus Gerardii*, *Glyceria* (*Puccinellia*) *maritima*, *Spergularia marginata* (*media*), *Suaeda maritima* var. *flexilis*, *Cochlearia anglica*, *Juncus obtusus*, and *Phalaris arundinacea*. So far as is known this is the first time such a community has been described for the East Anglian salt marshes. Transitions from salt to fresh-water marsh are frequent on the Atlantic coast of North America, and it is possible that previously they were more abundant in England, especially in the fenlands, but the influence of man and civilization has removed nearly all the traces of such transitions.

The abundance with which the different species occur on the various marshes has been computed and the results are shown in Table II. In each community a typical area was selected and a quadrat of the Clapham (1932) type thrown down at random. In two communities, a Salicornietum and Suaedeto-Salicornietum, permanent quadrats were established and remapped in successive years. The abundance was estimated by counting the number of plants in each quadrat and expressing the results as a percentage of the total

Table II

	Salicornia europaea agr.	Salicornia radicans var. lignosa	Suaeda maritima var. flexilis	Suaeda maritima var. macrocarpa	Aster tripolium	Glyceria maritima	Triglochin maritimum	Limonium vulgare	Spergularia marginata	(Obione portulacoides var. latifolia	Armeria maritima	Plantago maritima	Artemisia maritima	Juncus maritimus	Juncus Gerardi	Lepturus filiformis	Agrostis alba var. scolonifera	Pestuca rubra	Suaeda frutescens	Obione portulacoides var. parvifolia	Statice reticulata	Statice binervosa	Cochlearia anglica	Approximate level (I.Z.L.)
*Salicornietum, 1933	5	1	1	.	.	1	0.8
*Salicornietum, 1934	5	1	1	.	.	1	.	1	1	.	.	0.8
*Salicornietum, 1937	5	1	1	.	1	1	.	1	0.8
Asteretum	5	.	1	.	.	1	.	3	1	1	1	1	1.0
Closed marsh—G.S.M.	2	.	1	.	1	1	1	.	.	.	1	2.5
Late Asteretum	4	1	1	.	1	1	1	1	1	1	1	1	2.6
Late Asteretum	3	1	1	1	1	1	1	2	1	1	2	1	3	1	2.6
G.S.M.—open marsh	1	1	1	.	.	3	1	1	1	1	1	1	2.8
Sea meadow	1	1	1	.	.	1	1	1	1	1	1	1	2.8
Plantagnetum maritimae	2	1	1	1	1	1	1	1	1	1	1	4	.	1	3.3
Plantagnetum maritimae	2	1	1	1	1	1	1	1	1	1	1	2	.	1	3.3
Juncetum maritimae	1	1	1	.	.	1	2	1	1	1	1	1	.	1	1	1	2	1	3.4
Juncetum maritimae	1	.	.	.	1	.	1	1	.	1	1	2	.	2	1	1	.	1	3.4
Obioneto-Glycerietum maritimae	1	.	.	4	.	1	.	1	1	1	1	.	.	1.2
Obioneto-Statietum	3	.	.	1	.	.	.	1	1	2	1	.	.	2.8
reticulatae	1	1	.	1	1	.	2.7
Suaedeto-Statietum	1	.	.	4	1.1
reticulatae	3	.	.	3	1	1	1	.	1.1
†Suaedeto-Salicornietum, 1933	5	.	1	1	1	1	.	.	1.1
†Suaedeto-Salicornietum, 1934	3	.	.	.	1	1	1	.	.	1.1
†Suaedeto-Salicornietum, 1937	3	.	.	4	1	1	1	.	1.1

Abundance of species in different communities obtained by counting the number of plants in a square metre and calculating the percentage. Abundance expressed above in the usual notation, 1-5. Communities below the double line do not form a part of the Prisere. The communities of the Prisere are arranged above the double line in order of height.

* Same quadrat.

† Same quadrat.

number of plants in each quadrat. The percentages were then converted into the usual 1-5 notation. It will be seen that for most species there does not appear to be any definite correlation with level, at least not when using the accepted notation. *Salicornia europea* agg.¹ decreases with increasing height. *Limonium vulgare* is more abundant at lower levels than *Armeria maritima*, thus justifying a subdivision of the general salt-marsh community into an upper *Armerietum* and a lower *Limonietum*. This had been suspected previously from field observations. The table also suggests that the optimum conditions for *Suaeda maritima* vars. *flexilis* and *macrocarpa* and for *Obione portulacoides* var. *parvifolia* are independent of level and hence of submergence and exposure. However, these figures must be used with some caution because the areal percentage (area occupied by the plants) is often more important than number of plants per square metre. For example, in one quadrat a single plant of *Obione portulacoides* may occupy 60 % of the area, whilst there may be 200 plants of *Salicornia* which might only occupy 15 % of the total area.

The frequency with which certain species occur in the total number of quadrats from all the marshes has also been calculated, first as a percentage and then expressed in the usual 1-5 notation. These results are set out in Table III. The percentage frequency was then plotted against the average number of submergences per annum for each species, the latter figures being obtained from previous work (Chapman, 1934, 1938). The result of this operation is seen in Fig. 10, the continuous line representing the smoothed curve. It can be seen that there is a general correlation between frequency and submergence. There are, however, a few species which form exceptions, but these have not been included in the diagram. A study of this graph suggests that the following conclusions are justified:

(1) The species represented in Fig. 10 must be controlled to a considerable extent by the number of submergences they undergo, whereas the anomalous species are not controlled primarily by this factor, but must therefore be controlled by one or more other factors.

(2) The species which occur most widely over the marshes, e.g. those with the greatest frequency, nevertheless reach their greatest abundance on the lowest marshes. *Salicornia europaea*, *S. ramosissima*, and *Suaeda maritima* var. *flexilis* may be cited as the examples in Fig. 10.

(3) The species confined to the highest marshes, *Juncus maritimus*, *J. Gerardii*, *Lepturus filiformis*, *Agrostis alba*, *Festuca rubra* are not able to penetrate downwards on to the lower marshes, but the other species which attain dominance at low levels have been able to encroach upwards. The explanation of this distinction must be that the species on both the highest and lowest marshes can endure non-saline conditions, but that those species confined to the upper marshes cannot endure the more saline conditions which the lower

¹ This probably includes *Salicornia ramosissima* but the dwarf forms of this genus are not well known and it is difficult to be precise until a revision of the genus appears.

Studies in salt-marsh ecology

Table III

Species	Frequency	
	%	1-5 notation
<i>Salicornia europaea</i> agg.	94.45	5
<i>S. radicans</i> var. <i>lignosa</i>	11.1	1
<i>Suaeda maritima</i> var. <i>flexilis</i>	77.8	4
<i>Aster tripolium</i>	38.8	2
<i>Glyceria maritima</i>	60.05	4
<i>Triglochin maritimum</i>	50.0	3
<i>Limonium vulgare</i>	65.6	4
<i>Spergularia marginata</i>	50.0	3
<i>Obione portulacoides</i> var. <i>latifolia</i>	55.5	3
<i>Armeria maritima</i>	38.8	3
<i>Plantago maritima</i>	38.8	2
<i>Artemisia maritima</i>	5.5	2
<i>Juncus maritimus</i>	11.1	1
<i>J. Gerardii</i>	5.5	1
<i>Lepturus filiformis</i>	11.1	1
<i>Agrostis alba</i> var. <i>stolonifera</i>	5.5	1
<i>Festuca rubra</i>	5.5	1
<i>Obione portulacoides</i> var. <i>parvifolia</i>	5.5	1
<i>Suaeda fruticosa</i>	11.1	1
<i>Statice reticulata</i>	22.2	2
<i>S. binervosa</i>	11.1	1
<i>Cochlearia anglica</i>	33.3	1
	5.5	2
	5.5	1

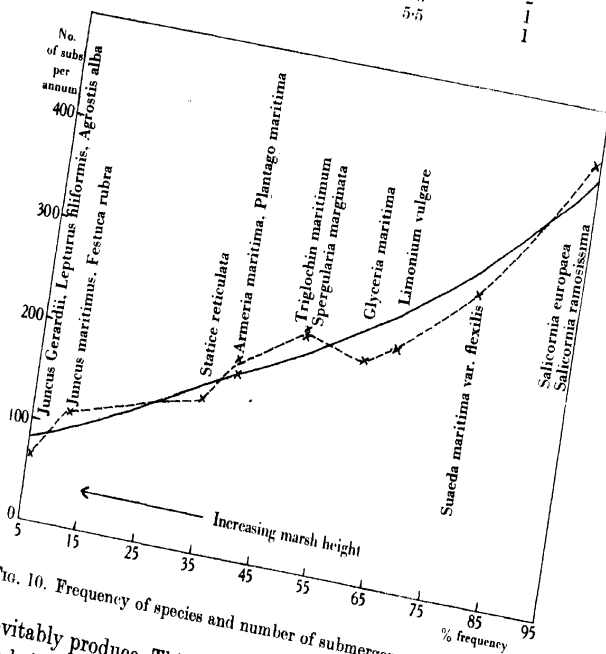


FIG. 10. Frequency of species and number of submergences per annum.

marshes inevitably produce. This effect of salinity in determining distribution is at present being confirmed by culture experiments on the different species, the results of which will be published in a later communication. At the same

time competition at the upper levels probably accounts for the decrease in numbers of those species which attain dominance at lower levels. The mechanism of this competition is at present under investigation.

The algal vegetation

The algae in many cases form communities which are as distinct as those of the phanerogams. Some of these communities have been recognized by other workers, and some are here described in detail for the first time.

Although the marshes form the principal areas occupied by the algal species, there are other habitats which bear algal floras differing from those found on the marshes. The creeks contain a flora the composition of which depends very largely upon their size and the nature of the bottom. The larger the creek and the more shingly the bed the richer will be the flora. This is strikingly illustrated in Norton Creek¹ at Brancaster Staithe where the mussel beds occur, but the same phenomenon appears on a smaller scale in the creeks that drain the various saltings. On the marshes there are also the salt pans which possess a typical flora. The evidence in favour of recognizing a separate salt pan flora has already been discussed in a previous paper and need not be repeated here (Chapman, 1937).

Algal salt-marsh communities

A zonation of algal communities with marsh level is not very obvious. Communities associated with pan margins or escarpments cannot be correlated with marsh height, since their presence depends on the existence of the physiographic features. In certain places, moreover, it is possible that substrate may determine the existence of a particular algal community, e.g. muddy Chlorophyceae (cf. p. 188). Edaphic conditions and marsh level, however, may not be the only factors determining the distribution of algae. Carter (1933), in her investigations of the Canvey and Dovey marshes, pointed out that species of *Enteromorpha*, *Rhizoclonium*, and *Vaucheria* are to be found at all levels. It is also true that some species of *Enteromorpha*, together with *Rhizoclonium implexum*, are scattered over all the Norfolk marshes, and in the case of such cosmopolitan algae Carter has suggested that it is the light and space relations which probably restrict their spread, rather than factors related to level or soil conditions.

It has proved extremely difficult to distinguish any clear zonation of algal communities with change of level, and therefore it is not proposed to divide them into two groups of upper and lower algal communities similar to those distinguished by Carter. At the same time the existence of the algal communities is unequivocal, and as such they probably have some ecological significance. At present the nature of this significance is not evident. It will be seen from the list of the different communities that rather more have been distinguished

¹ Maps of Scolt Head Island have appeared in recent volumes of the *Transactions of the Norfolk and Norwich Naturalists' Society* and also in the recent handbook (Cambridge, 1934).

at Scolt than at either Canvey or Dovey. A number of papers concerned with salt-marsh algal ecology have now been published, and the moment seems opportune for a summary of their results. At the end of this section, therefore, a survey will be made of all the algal communities so far distinguished, and a scheme prepared, which it is hoped will serve as a basis for future workers in this field.

I. *General Chlorophyceae associates*¹

Previous workers have differed considerably in their treatment of this community. Cotton (1912), in the Clare Island survey, distinguished four combinations which he classed as separate communities. Carter (1933), on the other hand, recognized the existence of only one community, which contained about the same number of species as the sum of those present in Cotton's four separate associations, and furthermore, she concluded that it could not be separated into the subcommunities. The present author agrees with Cotton in distinguishing several separate Chlorophycean combinations, but it is proposed to regard these as subdivisions of a single large associates equivalent to the General Chlorophyceae of Carter. This associates, in the form of one of the communities composing it, is represented on nearly every marsh, and under these circumstances it is not possible to correlate it with any particular level. The consocieties, on the other hand, are generally to be found in habitats distinguished by differences in the substrate, and therefore they may be edaphically determined.

(a) *Low sandy Chlorophyceae consocieties*

Enteromorpha prolifera f. capillaris	d. ²	Enteromorpha compressa	o.
Vaucheria Thuretii	l.	E. compressa f. complanata	o.
V. sphaerospora	o.	E. intestinalis f. flagelliformis	o.

This consocieties is confined to bare sandy places, and is generally associated with areas of soft sand into which one may sink ankle deep: it is scattered over the sand flats which stretch between the Far Point and Long Hills on Scolt Head Island. The nature of the habitats in which the community occurs suggests that its presence may be edaphically determined.

(b) *Sandy Chlorophyceae consocieties*

Enteromorpha torta	d.	Monostroma orbiculatum	f.
Rhizoclonium implexum	d.	Lyngbya aestuarii	f.
Enteromorpha compressa f. complanata	f.		(autumn)
E. prolifera f. capillaris	f.	Enteromorpha ramulosa f. robusta	o.
E. minima	f.	E. compressa	o.

¹ All the communities have been very briefly mentioned in a *Revision of the Norfolk Algae* (Chapman, 1937), but they are here described in full for the first time. The numbers given are the same as those used by Carter in describing similar communities on the Canvey and Dovey marshes. Communities II and VII are composed of diatoms and were not studied at Scolt.

² d. = dominant, f. = frequent, l. = local, o. = occasional, r. = rare.

<i>Urospora isogona</i>	o.	<i>Oscillatoria corallinae</i>	o.
<i>Rivularia atra</i>	o.	<i>Phormidium corium</i>	o.
<i>Rhizoclonium arenosum</i>	o.	<i>Nostoc Linckia</i>	o.
<i>Pelvetia canaliculata</i> forma libera	o.	<i>Microcoleus chthonoplastes</i>	l.
<i>Percursaria percura</i>	o.	<i>Acinetospora pusilla</i> var. <i>crinita</i>	l.
<i>Oscillatoria laetevirens</i>	o.	<i>Enteromorpha salina</i> f. <i>polyclados</i>	l.
<i>O. sancta</i>	o.	<i>E. micrococca</i> f. <i>tortuosa</i>	r.
<i>Vaucheria sphaerospora</i>	o.	<i>Rhizoclonium arenosum</i>	r.
<i>V. Thuretii</i>	o.	<i>Vaucheria coronata</i>	r.

This community covers a greater area than any other, since it is to be found on most of the marshes. Some of the species composing it only occur in certain areas; thus, *Lyngbya aestuarii* appears in quantity only on the higher marshes in the autumn, whilst *Enteromorpha salina* f. *polyclados* is very common on the bare sandy patches of the Hut marsh and Plantago marsh on Scolt Head Island. This community is also to be found around the edges of the lower marshes where the sand is firmer. In such places *Microcoleus chthonoplastes* is the principal blue-green alga, but no Phaeophyceae are present. The community is characterized nearly everywhere by the widespread occurrence of *Enteromorpha torta* and *Rhizoclonium implexum*, which in places may form an almost pure combination. The higher marshes, which in autumn are characterized by Cyanophyceae, also support *Monostroma orbiculatum* and *Percursaria percura* for most of the year. The two species of *Vaucheria* appear in different situations, *V. Thuretii* on the lower marshes, and *V. sphaerospora* on the upper. The distribution of these two species seems to be determined by the nature of the substrate: *V. Thuretii* is found more often on soft mud, such as that forming the banks of creeks, whereas *V. sphaerospora* is more often associated with the firmer mud of the higher marshes, and generally grows under and around phanerogams. In the Juncetum the flora is dominated by *Rhizoclonium implexum* with *R. arenosum* as a subdominant, but the other characteristic feature is the great development of the Cyanophycean component.

It is perfectly clear from what has been said that this algal community is not associated with any of the phanerogamic communities, since representative samples are to be found in most of the marsh communities. The most noticeable general feature is the gradual diminution of the different Chlorophyceae species with increasing height, so that on the upper marshes the community is represented mainly by *Enteromorpha torta* and *Rhizoclonium implexum*. These two species are cosmopolitan in range and it therefore seems as if they possess a tolerance towards a wide range of habitat conditions.

At the same time as the number of Chlorophyceae decrease, the number of Cyanophyceae tend to increase, and are most numerous on the higher marshes. However, it must be remembered that the presence of species such as *Lyngbya aestuarii* on higher marshes is closely correlated with season, autumn being the period when this and other forms are most abundant (cf. autumn Cyanophyceae community).

(c) *Muddy Chlorophyceae consocies*

<i>Enteromorpha prolifera</i> f. <i>capillaris</i>	d.	<i>Cladophora fracta</i> var. <i>flavescens</i>	o.
<i>Monostroma Grevillei</i> (vernal)	d.	<i>C. utriculosa</i>	o.
<i>Gomontia polyrhiza</i> (on shells)	a.	<i>C. flexuosa</i>	o.
<i>Cladophora fracta</i> var. <i>marina</i>	f.	<i>Enteromorpha compressa</i>	o.
<i>Enteromorpha torta</i>	f.	<i>E. compressa</i> f. <i>complanata</i>	o.
<i>Ulva lactuca</i>	f.	<i>Pilaiella littoralis</i>	o.
<i>Asperococcus fistulosus</i> (vernal)	f.	<i>Ectocarpus confervoides</i> var. <i>subulatus</i>	o.
<i>Phyllitis Fascia</i> (vernal)	f.	<i>Chaetomorpha linum</i>	r.
<i>Fucus vesiculosus</i> var. <i>evesiculosus</i>	f.	<i>Fucus platycarpus</i>	r.

This component of the General Chlorophyceae associates develops on areas where rather soft mud is predominant, and is often associated with *Zostera nana* and *Z. marina* var. *angustifolia*. In addition to the species enumerated above, others may be encountered that do not belong to this community, but which have been washed up by the tide. *Dumontia incrassata*, *Griffithsia flosculosa* and species of *Enteromorpha* are frequent drift forms. It is interesting to note that the species of *Cladophora* found in this community belong to that small group of *Cladophorae*, which, although attached in the early stages of their life history, become free-living for the latter part.

III. *Marginal Cyanophyceae consociation.*

<i>Oscillatoria sancta</i>	d.	<i>Oscillatoria formosa</i>	o.
<i>Phormidium autumnale</i>	d.	<i>Phormidium tenue</i>	o.
<i>Oscillatoria corallinae</i>	a.	<i>Spirulina subtilissima</i>	o.
<i>Phormidium corium</i>	f.-a.	<i>E. prolifera</i> f. <i>tubulosa</i>	l.a.
<i>Vaucheria Thuretii</i>	d.	<i>Pylaiella littoralis</i>	l.

This consociation flourishes at its best from the end of July to the end of October, appearing as a dark brown or blue-black mat over the mud banks of the creeks. In composition it is very similar to the community described by Carter for Canvey and Dovey. The area covered is usually confined to the upper portion of the creek banks, but in places the community may descend below the half-way mark. *Oscillatoria sancta* and *Phormidium autumnale* are the dominant species, but in places *Phormidium corium* may become a sub-dominant. One of the features of the marshes at Scolt Head Island is the comparative rarity, in spite of an intensive search, of species of *Spirulina*. The escarpments and the Juncetum form the only two areas from which they have been recorded. Many of the species composing this community are to be found sparsely throughout the year, but the algal mat, which indicates the presence of the community at its maximum growth, only appears in the late summer and autumn. *Vaucheria Thuretii* covers large areas of the creek banks and must be regarded as a co-dominant with the two Cyanophyceae. In the spring and summer the *Vaucheria* alone is dominant but in autumn the Cyanophyceae cover the whole area. For this reason the *Vaucheria* has been retained in this community and not considered as forming a separate one.

IV. *Ulothrix socies*.

<i>Ulothrix speciosa</i>	d.	<i>Enteromorpha minima</i>	o.
<i>Urospora isogona</i>	f.-a.	<i>Rhizoclonium implexum</i>	o.
<i>Ulothrix flacca</i>	o.	<i>Ulothrix implexa</i>	r.

The species from which this community derives its name are found principally in spring, and so the community must be regarded as essentially vernal. In many places only the dominant species, *Ulothrix speciosa*, is represented. The community occurs in the stony beds of creeks so long as there is no standing water present during low tide, and also on the vegetation bordering the smaller creeks of low marshes. It is easily recognizable by the silky nature of the threads which form a bright green carpet when the community attains its maximum growth. Towards summer the dominance of *Ulothrix speciosa* seems to be replaced by that of *Urospora isogona*, which is principally an aestival species. After the disintegration of this community, which commences in April, the stony beds of the smaller creeks often remain bare, whilst the muddy creek banks become covered with *Urospora isogona*, *Rhizoclonium implexum*, and *Enteromorpha minima*.

V. *Enteromorpha minima socies*.

<i>Enteromorpha minima</i>	d.	<i>Ulothrix flacca</i>	o.
<i>E. prolifera</i> f. <i>tubulosa</i>	f.	<i>Vaucheria sphaerospora</i>	o.
<i>E. clathrata</i> f. <i>prostrata</i>	f.	<i>Enteromorpha micrococca</i> f. <i>tortuosa</i>	l.
<i>Rhizoclonium implexum</i>	o.-a.	<i>Bostrychia scorpioides</i>	l.

This community generally grows epiphytically upon the vegetation bordering the creek banks, or, more rarely, it may cover the ground along the edges of creeks. In most places *Enteromorpha minima* is the only species present, but on the lower marshes (Asteretum, creek Asteretum, and late Asteretum) *Enteromorpha prolifera* f. *tubulosa* is frequently associated with it. On the higher marshes (general salt marsh, Plantaginetum, and sea meadow communities) the role of subdominant is played by *Enteromorpha clathrata* f. *prostrata*. *Vaucheria sphaerospora* has a local distribution, generally being found under *Obione* bushes where the creek banks are rather higher than usual, and in such places some sand is usually admixed with the mud: therefore either height or soil conditions might determine the presence of this species. *Enteromorpha micrococca* f. *tortuosa* can usually be found in this community when it appears in the creek Asteretum. Wherever *Obione portulacoides* fringes the creeks, the stems form a foothold for *Enteromorpha minima* throughout the year, and the alga hangs from it in festoons. In the winter and spring the remains of *Aster* and *Salicornia* plants also form a substrate upon which *Enteromorpha minima* grows. In the winter months only young plants of *E. minima* are to be found and *Rhizoclonium implexum* is the dominant species of the community. Occasionally, examples of this community may be found growing on the stems of *Obione*, and on old *Salicornia*, *Limonium*, and *Aster* plants in the open marsh away from any creek.

VI. *Gelatinous Cyanophyceae society.*

<i>Nostoc commune</i>	d.	<i>Rivularia atra</i>	o.
<i>Phormidium molle</i>	o.	<i>Phormidium corium</i>	r.

The name given to this community is based on the character of the dominant species, which in this case is *Nostoc commune*. The community attains its maximum development along the edges of low stable shingle laterals. The *Nostoc* colonies are flabby masses of jelly lying curled and twisted upon the ground. They are particularly prominent after rain or after flooding by a spring tide. In dry weather the colonies shrivel up to small black crinkled masses, and under these conditions the community is liable to be overlooked. In height the community is largely confined to areas that are near high-water mark, and therefore it is only a flooded comparatively few times during the year. It is not a seasonal community but may be found throughout the whole of the year.

VIII. *Autumn Cyanophyceae consocies.*

<i>Lyngbya aestuarii</i>	d.	<i>Phormidium autumnale</i>	f.
<i>L. aestuarii</i> var. <i>spectabilis</i>	d.	<i>Lyngbya majuscula</i>	o.
<i>Oscillatoria nigroviridis</i>	f.	<i>L. confervoides</i>	o.-f.
<i>Chroococcus turgidus</i> var. <i>maximus</i>	f.	<i>Microcoleus chthonoplastes</i>	o.

This consocies is characteristic of the upper levels and is associated with the open marsh, occupying every available inch of ground between the phanerogamic species. It develops towards the end of July and may be found up to November, or in some places up to March, whilst isolated samples of the component species can be encountered at all times of the year. The phanerogamic communities in which it appears are the general salt marsh, the sea meadow, Obioneto-Staticetum and Obioneto-Glycerietum and to a lesser extent in the Plantaginetum. The characteristic nature of the community is its brownish black colour and felt-like appearance, whilst on microscopic examination the observer is struck by the overwhelming dominance of *Lyngbya aestuarii* and its variety *spectabilis*. The community also covers the pans in autumn, and in these circumstances the abundance of *Chroococcus turgidus* var. *maximus* is of interest. This species does not play such an important part on the Canvey and Dovey Marshes as it appears to do in Norfolk, but it is, however, recorded as frequent on the Lough Ine marshes. Another noteworthy feature is the comparative rarity of *Lyngbya majuscula* and *L. confervoides* as compared with Canvey and Dovey.

IX. *Phormidium autumnale socies.*

<i>Phormidium autumnale</i>	d.	<i>Calothrix pulvinata</i>	l.-l.a.
<i>P. corium</i>	f.	<i>Pilinia rimosa</i>	o.
<i>P. papyraceum</i>	a.		

This socies is confined to the Obionetum fringing the creeks of the marshes from the Asteretum up to the sea meadow, where it grows on the ground and also spreads over the stems of the *Obione portulacoides*. In some places

Phormidium corium may become subdominant. In yet other places, usually on *Obione* and *Suaeda* stems near shingle ridges, *Calothrix pulvinata* becomes locally dominant, forming a distinct society. The community exists throughout the year but attains its best development in the damp winter months.

X. *Rivularia*-*Phaeococcus* *societis*.

<i>Rivularia atra</i> var. <i>confluens</i>	d.	<i>Calothrix scopulorum</i>	f.
<i>R. atra</i>	f.	<i>Vaucheria sphaerospora</i>	f.
<i>Phaeococcus adnatus</i>	f.-a.	<i>Endoderma perforans</i>	o.-l.f.

This *societis* is usually confined to the upper marshes where it is to be found near the periphery. *Rivularia atra* and its variety occur throughout all the year, but *Phaeococcus adnatus* appears to show some seasonal fluctuation, being more abundant in the autumn and winter. *Phaeococcus* may be scattered over the soil uncontaminated by other algae, but more frequently it is associated with the *Calothrix*, the combination of the two appearing as irregular light-brown lumps. *Vaucheria sphaerospora* only enters this community when bushes of *Suaeda fruticosa* are present. *Endoderma perforans* is usually associated with the *Rivularia* colonies and only becomes evident when a colony is teased apart under the microscope; it may also appear by itself on the bare soil, whereas on the Canvey and Dovey marshes it was rarely separate from the colonies of *R. atra*.

XII. *Catenella*-*Bostrychia* *consocietis*.

<i>Catenella repens</i>	d.	<i>E. clathrata</i> f. <i>prostrata</i>	a.
<i>Bostrychia scorpioides</i>	d.	<i>E. minima</i>	o.
<i>Enteromorpha prolifera</i> f. <i>tubulosa</i>	a.		

This *consocietis* is of interest in that it appears in two forms on these marshes. The first is a pure association of the two dominants, and it occurs under *Suaeda fruticosa* bushes where they line lateral ridges bounding the higher marshes (late Asteretum and above). The characteristic feature of this form of the community is the dwarf nature of the *Catenella*, which is embedded in the ground like a moss. Dwarf *Catenella repens* may also be found growing epiphytically upon the stems of *Plantago maritima* and *Armeria maritima* as at Clare Island (Cotton, 1912). In these habitats the community probably exists in conditions very similar to those operating over the Dovey, Canvey, and Clare Island marshes. The second facies of this community, however, must undergo far more frequent submergence since it is to be found under the plants of *Obione portulacoides* which fringe the creeks, occurring from the late Asteretum up to the sea meadow stage. A distinguishing feature is the rank nature of the *Catenella*, which either grows on the soil, or more frequently as an epiphyte on the stems of the *Obione*. In one or two areas along the banks of creeks this community may develop into another form in which *Catenella repens* is largely replaced by *Enteromorpha prolifera* f. *tubulosa* or *E. clathrata* f. *prostrata*.

XIII. *Pelvetia-Bostrychia consocies*.

<i>Pelvetia canaliculata</i> forma libera	d.	<i>E. minima</i>	o.
<i>Bostrychia scorpioides</i>	d.	<i>Fucus vesiculosus</i> ecad caespitosus	l.
<i>Enteromorpha prolifera</i> f. <i>tubulosa</i>	a.-f.		

So far, a community like this has never been described in detail for any other marsh area that has been investigated ecologically, although a form of it may exist on the Lough Ine marshes (cf. p. 197). The first traces of this consocies can be seen in the *Salicornietum*, but it attains its maximum development in the *Asteretum*, where it may cover all the available space between the phanerogams, and finally it disappears in the G.S.M. community. In Norfolk, tremendous areas on the lower marshes are covered by this community, and when it is present the growth of the two species composing it is so great that no other alga can exist. In the *Asteretum* the community may be represented by *Pelvetia* only, whilst on slightly higher marshes (late *Asteretum*) the community may be represented by *Bostrychia scorpioides* and *Enteromorpha prolifera* f. *tubulosa* only. It seems probable that with increased height the place of *Pelvetia* is taken by the *Enteromorpha*. *Bostrychia scorpioides*, on the other hand, occurs over the whole range of the community, and therefore is probably more tolerant towards the environmental conditions.

XIV. *Enteromorpha clathrata socies*.

<i>Enteromorpha clathrata</i> f. <i>prostrata</i>	d.	<i>Enteromorpha torta</i>	o.
<i>E. prolifera</i> f. <i>tubulosa</i>	o.	<i>Calothrix endophytica</i>	o.

This again is another community which has not yet been described from other areas. This is because the dominant species is either unrecorded, or else it does not play such a prominent part as it does on the Norfolk marshes. During a visit to the marshes at Hampden Water and Mersea Island, this same dominant species was found but time did not permit of an investigation into the associated algae. It is possible, therefore, that this socies may be present on the Essex marshes. When the species was first encountered it was thought to be the form *Enteromorpha prolifera* var. B I, described by Carter (1933), but on further examination, it was finally decided that the plant was a form of *Enteromorpha clathrata*. The community is mainly confined to the G.S.M. and *Plantaginetum* and hence has a comparatively restricted range. In places it merges with Community XII, especially near the banks of small creeks, but in general, it is to be found on the open marsh away from creeks. Where the community occurs in isolated parts of the Great *Obione* fringe, *Enteromorpha torta* often contains *Calothrix endophytica* living endophytically inside the tubes. In the autumn the bare soil of the G.S.M. and *Plantaginetum* stages is occupied by Community VIII, with the result that this community is probably not so sharply distinguished as those previously described.

XV. *Fucus limicola consocies*.

<i>Fucus vesiculosus</i> ecad <i>caespitosus</i>	d.	<i>Rhizoclonium implexum</i>	o.
<i>F. vesiculosus</i> ecad <i>volubilis</i>	d.	<i>Enteromorpha micrococca</i> f. <i>tortuosa</i>	o.
<i>F. vesiculosus</i> ecad <i>muscoides</i>	l.a.	<i>E. prolifera</i> f. <i>tubulosa</i>	o.-f.
<i>Enteromorpha prolifera</i> f. <i>capillaris</i>	o.	<i>E. clathrata</i> f. <i>prostrata</i>	o.
<i>Pelvetia canaliculata</i> forma libera	o.	<i>Acinetospora pusilla</i> var. <i>crinita</i>	l.r.
<i>Enteromorpha torta</i>	o.	<i>Bostrychia scorpioides</i>	l.
<i>E. minima</i>	o.		

In the *Salicornietum*, *Fucus caespitosus* is the dominant form, and in places may be sufficiently abundant to form a pure *societ*. Where, however, a marsh abuts on a major creek, *Fucus volubilis* appears as a co-dominant, and in some places as the dominant. It is in these areas, also, that the other associated species are most abundant, except the variety of *Enteromorpha clathrata* which only occurs on the higher marshes. When investigating this community one has to be careful in distinguishing species which really belong to it from those which have been thrown up. Near the edges of major creeks plants of many species, which have been torn from their anchorings in the creeks, are washed up and trapped by the vegetation and there they may remain in a fresh state for some time. Continual acquaintance with the community for a long period is essential in order to determine its true components.

In the *Plantaginietum* a *societ* can be distinguished, which is dominated by a form which is probably *Fucus vesiculosus* var. *muscoides*.

XVI. *Pan association*.

This community comprises all species recorded as being typical of pans throughout the marshes (cf. Chapman, 1937).

Ecological distribution

The distribution of the algal communities may be investigated from two aspects, those of time and space.

Distribution in time. This is best studied from Fig. 11 and there is very little in it that requires comment. In Community I *b* (sandy Chlorophyceae) the Chlorophyceae component attains to its maximum development in summer, and the Cyanophyceae constituent in autumn. The gelatinous Cyanophyceae (Community VI) is misleading in the field, because in the summer the dried up colonies are apt to be overlooked, and hence its seasonal distribution wrongly recorded. Compared with Carter's results both Communities V (*Enteromorpha minima*) and VI show a more extended range than at either Canvey or Dovey. In the case of VI this might be expected as the dominant species are different (*Anabaena* in one and *Nostoc* in the other). Community V at Canvey and Dovey has a winter maximum, but in Norfolk this only appears in the late winter and early spring. This maximum is brought about by the growth of *Enteromorpha minima* and *Ulothrix flacca* on dead plant remains. Community X (*Rivularia-Phaeococcus*) at Canvey and Dovey attains to a maximum in the autumn, and on casual inspection a similar condition might be thought to exist

in Norfolk. It became clear, however, that the *Rivularia* component of this community is equally abundant in summer, but it is liable to be overlooked because it becomes covered with a deposit of salt through the evaporation of the surface soil water. This salt deposit covers all the ground, including the *Rivularia* colonies, which therefore only become evident when the deposit is removed. The *Phaeococcus* component of this community, on the other hand, does decrease during the summer months. The other communities need no

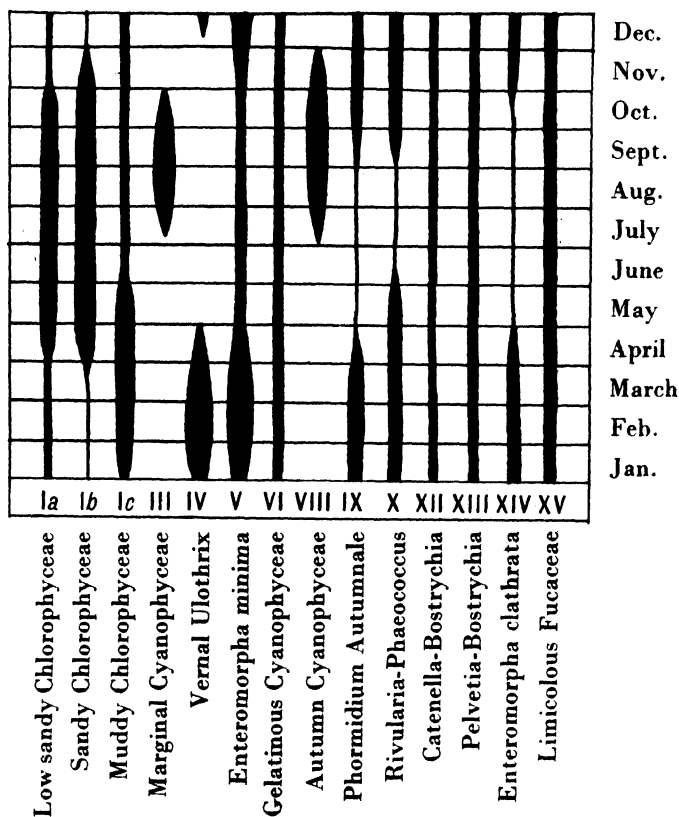


FIG. 11. Distribution of the Norfolk salt-marsh algal communities in time.

further explanation, except to say that the decrease in Community XIV (*Enteromorpha clathrata*) is probably due to the greater exposure during the summer months with the consequent greater degree of desiccation.

Distribution in space. From Fig. 12 it will be seen that Community I b (sandy Chlorophyceae) possesses the widest range, whilst VIII (autumn Cyanophyceae) and XII (*Catenella-Bostrychia*) also occur in five different habitats, whilst Communities X (*Rivularia-Phaeococcus*) and XV (Limicolous Fucaceae) are recorded from four. Most of the communities occur over a range of one to three habitats, although five algal communities are associated with

one particular habitat. The problem to be solved in these cases, therefore, is the nature of the relationship. Three possibilities may be suggested:

(1) The algae are associated with the Phanerogamic vegetation. Community IX (*Phormidium autumnale*) may represent this possibility as it is probably associated with the presence of *Obione portulacoides*.

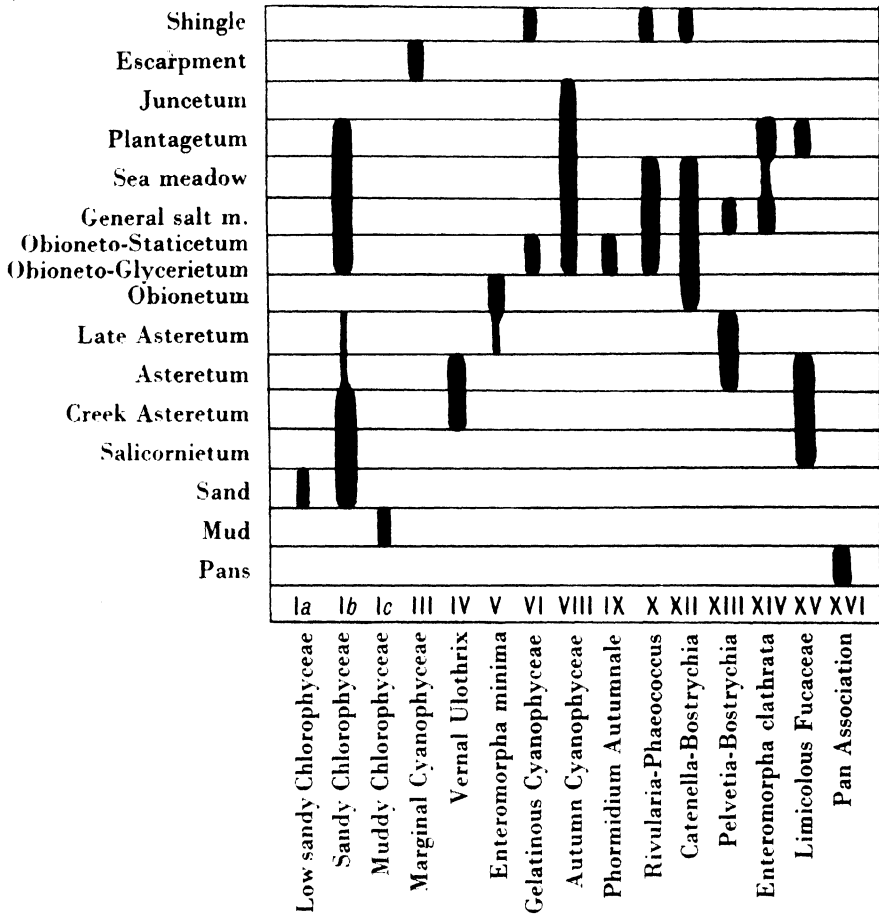


FIG. 12. Distribution of the salt-marsh algal communities on Norfolk marshes in space.

(2) The algae are dependent upon the edaphic conditions. This is probably the case with Communities Ia (low sandy Chlorophyceae) and Ic (muddy Chlorophyceae).

(3) The presence of the algae is due to the physical character of the environment, e.g. slope, exposure, wave-action. Here Communities III (marginal Cyanophyceae) and XV (Limicolous Fucaceae) may be tentatively suggested as being composed of species which probably can withstand exposure and wave action.

It must be remembered that these are suggestions, and their validity can only be proved by experiments in the field which it is hoped will be carried out soon.

Comparison with other salt-marsh areas

Carter in her survey (1933, 1934) of the Canvey and Dovey salt marshes pointed out that two factors may determine the differences between the algal floras of separate salt-marsh areas. These two factors are:

- (1) Differences in the phanerogamic vegetation.
- (2) Light and space relations, which are largely controlled by the phanerogams.

Whilst these two factors may play an important part in determining the algal floras, it would perhaps be premature to consider them as the only two factors operating. Evidence obtained from Scolt suggests that tidal range and height above mean sea-level, operating through the frequency and duration of submergence and exposure together with a salinity component may play some part in determining, not only the ranges of the species, but also their presence or otherwise.

Dovey salt marshes. On the Norfolk marshes *Fucus vesiculosus* *ecad caespitosus* is usually the dominant alga in the Salicornietum, whereas on the Dovey marshes it is *Enteromorpha* spp.

At the Dovey the algal flora of the Glycerietum (which appears to correspond in level to the Asteretum at Scolt) is dominated by *Vaucheria*, whilst in summer, Cyanophyceae are frequent. The Asteretum at Scolt bears a totally different algal vegetation, the explanation probably being the difference in the phanerogamic species, although the level of the two communities in relation to the tides may be important. This last suggestion cannot be confirmed at present, as there are no adequate data available from Wales. There is also no evidence on the Dovey marshes of an autumn Cyanophyceae community. The algal vegetation of Juncetum communities in the two areas is by no means similar: *Bostrychia scorpioides* and *Catenella repens* are recorded from the Dovey and their absence from the same community in Norfolk cannot be due to difference of vegetation or light supply. It may be connected with relative differences in the marsh heights above mean sea-level.

Essex salt marshes (Canvey). The autumn Cyanophyceae occur on low marshes in this area, even in the Salicornietum. Among the Chlorophyceae it is apparently rare to find *Rhizoclonium* associated with *Enteromorpha*. There does not appear to be anything comparable to the huge areas covered by the *Pelvetia canaliculata* forma *libera*-*Bostrychia scorpioides* community which is so prominent in Norfolk. This is somewhat surprising in view of the proximity of the two areas. The Obionetum at Canvey and in Norfolk has some common features, but *Catenella repens*, so typical in Norfolk, is absent from this community at Canvey.

Clare Island. The bare sand flats possess a green flora dominated by *Rhizoclonium riparium*, whereas in Norfolk the algal ropes of the bare sand flats are generally dominated by *Enteromorpha* spp. although *Rhizoclonium implexum* may be present. One of the most interesting, but so far inexplicable, facts in Norfolk is the overwhelming dominance of *Rhizoclonium implexum* and the comparative rarity of *R. riparium*, which in other areas appears to be far more frequent either under its own name or as a variety of *R. hieroglyphicum*. As on the Dovey marshes the autumn Cyanophyceae develop on low marshes in the winter. *Fucus vesiculosus* ecad *muscoides* occurs on the Clare Island marshes at a lower level than it does in Norfolk. This difference of level may provide a clue to the factors controlling its appearance.

Lough Ine marshes. These have been described by Rees (1935) who regards them as retrogressive marsh phases which are slowly disappearing. The vegetation is that of general salt marsh and Juncetum. *Limicolous* *Fucaceae* have been recorded including all the species found at Scolt, with *Fucus spiralis* var. *nana* in addition. Gelatinous Cyanophyceae also occur, but the dominant species are different, *Aphanothece pallida* and *Gloeocapsa crepidinum*. *Rivularia nitida* is very frequent on these marshes, whilst I have never seen this species on the Norfolk marshes.

It is apparent from this survey of three different marsh areas, that there seems to be no common scheme of algal distribution; such species as are found, and the situations in which they occur, probably being determined very largely by special local conditions. The comparison of the different communities from the various areas demonstrates clearly that while there may be resemblances between two places for one set of marshes, for another set the resemblance may lie between two other areas. Thus, marsh 1 at A may resemble marsh 2 at B, whilst marsh 2 at A resembles marsh 2 at C.

Pans, channels and escarpments. On the Dovey and Canvey marshes Carter has found that pans which are full of water all the year round have no persistent algal flora, whilst it has already been pointed out that a pan algal flora can be recognized in Norfolk.

The margins of the pans on the Dovey and Canvey salt marshes formed a good locality for blue-green algae, especially *Rivularia atra*. This species has rarely been found in such a place in Norfolk, and when Cyanophyceae are present they are the typical autumn species. In silting pans, colonization at Canvey and Dovey is begun by the blue-green algae and is followed by *Vaucheria*, but at the Dovey a *Rhizoclonium riparium* stage is interpolated. In Norfolk, silting pans may bear *Microcoleus chthonoplastes*, but the principal colonists are probably Chlorophyceae, with the exception of *Vaucheria* spp. In all the areas *V. Thuretii* is the typical colonist of the creek banks. The escarpments of the Canvey, Dovey, and Clare Island marshes all have a flora which differs from the mud steeps of Norfolk in the presence of *Rivularia* species. This may be because the escarpments in the former areas are generally

formed of peat, whilst in Norfolk they are built of mud which is much more susceptible to erosion. At Clare Island and Lough Ine it has even proved possible to distinguish four zones on the escarpments.

Pioneer algae. Carter does not regard the algae as playing an important pioneering part in the Dovey marshes, but at Canvey, Cyanophyceae and *Vaucheria* are primary colonists followed by *Salicornia herbacea*. On Clare Island *Rhizoclonium riparium* is the primary colonist, and is followed by phanerogams. At Scolt, species of *Enteromorpha* are the principal pioneers, although in soft mud areas *Fucus vesiculosus* var. *evesiculosus* may play some part. Along the main creeks *Vaucheria Thuretii* acts as primary colonist binding the mud. There is, therefore, no pioneering species among the algae common to all these various marsh areas. Each area must therefore be investigated and studied on its own merits.

Survey of the salt-marsh algal communities

There seem to be an increasing number of papers dealing with the algal communities of salt marshes, and since each investigator not unnaturally uses his own nomenclature the problem will soon become confused, because many communities, which are essentially the same, will be given different names. A survey of the existing state of knowledge therefore appears desirable, and, if possible, a scheme should be formulated in which the communities so far recognized are given definite names, the future use of which should prevent further confusion. An attempt has been made to carry out this survey and it remains to suggest the basis upon which the different communities should be recognized. For this purpose Table IV has been drawn up, wherein the communities recorded from four different areas are noted, and it also contains a column in which the names proposed for future use are set out. The comparison of the four areas requires little further comment. It does, however, emphasize the apparent widespread nature of Communities I, X, and XII, which appear in all four areas. It also shows that the marginal Cyanophyceae, gelatinous Cyanophyceae, and *Fucus limicola* communities have a fairly wide distribution, since they appear in at least three of the areas. This suggests that in the case of Communities I, X, and XII, the species composing them must be tolerant of widely different conditions, particularly when it is remembered that the areas represent the west coasts of Ireland and Wales and the east coast of England. The same cannot be said of Communities III and VI since the dominant species are not always the same.

The following features in the last column may require some explanation. It is proposed that there should be a general Chlorophyceae associates divisible into three consocieties, the low sandy Chlorophyceae, the sandy Chlorophyceae, and the muddy Chlorophyceae. With the sole exception of the general Chlorophyceae associates it is proposed that all the other algal combinations should be regarded as either consocieties or societies. These communities usually occupy such

Table IV. *Salt-marsh algal communities*

No.	Scott Head Island General Chlorophyceae	Canvey and Dovey General Chlorophyceae	Clare Island	Lough Ine, Ireland	Communities. Suggested nomenclature
I			—	—	General Chlorophyceae
I a	Low sandy Chloro- phyceae	—	—	—	Low sandy Chlorophyceae consociates
I b	Sandy Chlorophyceae	—	Sandy Chlorophyceae	Filamentous algae	Sandy Chlorophyceae consociates
I c	Muddy Chlorophyceae	—	Muddy Chlorophyceae	—	Muddy Chlorophyceae consociates
II	Probably present. Not investigated	Marginal diatoms	—	—	Marginal diatom con- sociation
III	Marginal Cyanophyceae	Marginal Cyanophyceae	?	Vertical banks ass.: (a) <i>Rhizoclonium</i> . <i>Phor-</i> <i>midium</i> band (b) <i>Ulothrix</i> . <i>Phor-</i> <i>midium</i> band	Marginal Cyanophyceae consociation
IV	<i>Ulothrix</i> community	<i>Ulothrix flacca</i> com- munity	—	—	Vernal <i>Ulothrix</i> societies
V	<i>Enteromorpha minima</i> community	<i>Enteromorpha minima</i> . <i>Rhizoclonium</i> com- munity	—	—	<i>Enteromorpha minima</i> societies
VI	Gelatinous Cyano- phyceae	<i>Anabaena torulosa</i> community	—	—	Gelatinous Cyanophyceae societies or society depend- ing on permanence
VII	Probably present. Not investigated	Filamentous diatoms	—	—	Filamentous diatom consociates
VIII	Autumn Cyanophyceae	Autumn Cyanophyceae	—	—	Autumn Cyanophyceae consociates
IX	<i>Phormidium autumnale</i> community	<i>Phormidium autumnale</i> community	—	—	<i>Phormidium autumnale</i> societies
X	<i>Rivularia-Phaeococcus</i> community	<i>Rivularia-Phaeococcus</i> community	—	—	<i>Rivularia-Phaeococcus</i> societies
XI	—	<i>Pelvetia muscoides</i> community	<i>Rivularia-Phaeococcus</i> association	—	<i>Pelvetia muscoides</i> societies
XII	<i>Catenella-Bostrychia</i> community	<i>Catenella-Bostrychia</i> community	—	—	<i>Catenella-Bostrychia</i> consociates
XIII	<i>Pelvetia-Bostrychia</i> community	—	—	—	<i>Pelvetia limicola</i> consociates
XIV	<i>Enteromorpha clathrata</i> community	—	—	—	<i>Enteromorpha clathrata</i> societies
XV	<i>Fucus limicola</i> community	—	<i>Fucus limicola</i> association	—	<i>Fucus limicola</i> consociates
XVI	Pan community	—	—	—	Pan association

a relatively small area that one is not justified in regarding them as associates in the ecological sense. The term marginal Cyanophyceae is perhaps more satisfactory as a name, rather than utilizing the name of the dominant species to designate it, especially since the community is recognized by habitat as well as by the species composing it. In the different areas the community may appear in the same position but its composition may vary slightly. For the same reason Community IV is termed the vernal *Ulothrix* societies because, though similar in occurrence, the composition may show some variation in different areas. Further complications are only added if a number of *Ulothrix* communities are distinguished, each recognized by the dominant species. Communities VI, XI, and XV have been given general names for the same reason. Communities V, VIII, IX, X, and XII retain the names of the dominant species since their composition seems to vary but little, and in all the areas the dominant species is the same. Under these circumstances it is permissible to use the name of the dominant species as a cognomen for the community. The pan association comprises all the species that may occur permanently in pans, and if subdivisions are desirable they should be regarded as ecologically equivalent to consociations and societies, since they will occupy such very restricted habitats.

In drawing up the list of names proposed for general use, the main idea has been to use, so far as possible, names that have already been adopted. In this way further confusion may be prevented, and the undesirable practice of introducing a whole set of new names is avoided. It is sincerely hoped that this survey and the suggestions emanating from it will be acceptable to workers in this field, and that it will form a sound basis for use in further studies of salt-marsh algal communities.

In concluding these five sections I desire to offer my thanks primarily to Dr H. Godwin for his untiring enthusiasm in discussing, criticizing, and reading through the results of these studies and also for many valuable suggestions throughout the investigation. My thanks are also due to Prof. Debenham, Mr Steers, Dr Long, and the Watcher at Scolt Head Island (Charles Chestney) for the various facilities they have afforded me during the course of this investigation. These studies were carried out whilst the author was Frank Smart Student in Botany at Gonville and Caius College, Cambridge.

REFERENCES

- Adriani, E. D.** "Recherches sur la Synécologie de quelques Associations halophiles Méditerranéennes." *Stat. Intern. Géobot. Méd. et Alp. Montpellier Comm.* **32**, 1934.
- Carter, N.** "The algal ecology of two salt marshes." *This JOURNAL*, **22**, **23**, 1933, 1934.
- Chapman, V. J.** *The Ecology in Scolt Head Island Handbook*. Cambridge, 1934.
- Chapman, V. J.** "The halophyte problem in the light of recent investigations." *Quart. Rev. Biol.* **2**, 1936.
- Chapman, V. J.** "A revision of the marine algae of Norfolk." *J. Linn. Soc. (Bot.)*, **51**, 1937.
- Chapman, V. J.** "Studies in salt-marsh ecology. Parts I-III." *This JOURNAL*, **26**, 1938.

- Clapham, A. R.** "The form of the observational unit in quantitative ecology." *This JOURNAL*, **20**, 1932.
- Cotton, A. D.** "Clare Island Survey. XV. Marine algae." *Proc. R. Irish. Acad.* **31**, 1912.
- Morss, W. L.** "The plant colonization of Merse lands in the estuary of the River Nith." *This JOURNAL*, **15**, 1927.
- Nichol, E. A. T.** "The ecology of a salt marsh." *J. Mar. Biol. Ass. U.K.* **21**, 1935.
- Rees, T. K.** "The marine algae of Lough Ine." *This JOURNAL*, **23**, 1935.
- Salisbury, E. J.** "Notes on edaphic succession in some dune soils with special reference to the time factor." *This JOURNAL*, **13**, 1925.
- Schratz, E.** "Beiträge zur Biologie der Halophyten." *Jb. wiss. Bot.* **80, 81**, 1934.
- Steiner, M.** "Oekologie der Salzmarschen der Nordöstlichen Vereinigten Staaten von Nordamerika." *Jb. wiss. Bot.* **81**, 1934.
- Wright, C. H.** *Soil Analysis*. London, 1934.

Note. The authorities for the algal species cited are those found in Newton's *Handbook of the British Marine Seaweeds* (1931) and for the Cyanophyceae, Geitler in Rabenhorst's *Kryptogamen Flora* (1932).

THE OAKWOODS (QUERCETUM SESSILIFLORAE) OF KILLARNEY, IRELAND

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(With Plates V and VI and nine Figures in the Text)

THE descriptions and conclusions to be found in this paper are the result of work carried out from a camp at Queen's Cottage, Killarney, in August and September 1936. The authors are very greatly indebted to the following members of the Cambridge Botany School, who were in the party and who all, in various ways, contributed to the preliminary survey, to the routine observations and to the discussion of the problems which arose: A. Burges, Verona M. Conway, G. C. Evans, P. W. Richards, Anne Richards, D. H. Valentine, E. F. Warburg.

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INTRODUCTION

The flora of western Ireland is rich in species with a peculiar distribution in the northern hemisphere. Against a background of fairly wide-ranging species of central and western Europe are to be found representatives of the North American, Lusitanian and Mediterranean floras, as well as arctic alpinas and species whose centres of distribution are in the tropics and subtropics. To the plant geographer this topsy-turvy mixture presents the interesting problem of how and when the species arrived. With this mixture we are not now concerned, except in so far as it is an expression of an extremely tolerant climate.

In contrast with the floristic variety, we find that the major plant communities, in particular the climax oakwoods, are those of the mean or normal climate of the British Isles. Very few of the rare Irish species go to the making of the Killarney oakwoods, a reminder that most of these species are to be found in the seral stages of the vegetation, or in specialized habitats. The interest of these woods, then, lies not so much in their floristic composition—except as regards ferns and bryophytes—but rather in the abundance and vigour of certain species common enough in western Europe and so favoured here by climate that they play an important part in the woodland structure. Most of these species are evergreen. The dominant tree (*Quercus sessiliflora*) is deciduous, but the evergreen holly (*Ilex aquifolium*) is so abundant in one facies of the oakwood that it forms a continuous layer, and in the others it is present in large numbers. In the more open parts of the woods *Calluna vulgaris* and *Vaccinium myrtillus* form a dwarf shrub layer growing with a vigour and attaining a size perhaps found nowhere else in the British Isles. Most of the herbaceous species are also evergreen or partly so and the whole effect is enhanced by the carpet of bryophytes and *Hymenophyllum* covering the boulders and tree trunks and reaching far into the tree crowns. Thus from the species available in the neighbourhood there has been formed a community closely approaching an evergreen hygrophilous forest.

The Killarney oakwoods (Fig. 1) are situated in a district noted for its scenic beauty, due in no small measure to the well-wooded slopes of the rugged mountains surrounding the Upper Lake. The lake itself lies at about 21 m. (70 ft.) above sea-level and the mountains form a rim to its basin on the west, south and east, rising in the west to 910 m. (3000 ft.) at Carrauntoohil, the highest mountain in Ireland. The woods show a well-marked altitudinal limit at 180–240 m. (600–800 ft.), which Praeger (1934) regards as natural and undisturbed—a limit set by climate. Much of the basin below this level is occupied by vegetation of the moorland or heath type. The most frequent dominant on the wet peaty slopes is *Molinia coerulea*, while *Calluna vulgaris* and *Ulex gallii* are co-dominant on drier ground. Many of the low-lying woods have a sharp boundary where they abut on the *Molinietum*.

Irish foresters are of the opinion that no planting of oak or sowing of acorns has ever been done in this neighbourhood. Other species have been planted; there is a plantation of beech (*Fagus sylvatica*) at 120 m. (400 ft.), and the trees are regenerating, though poorly. Nearer Killarney town and in the demesne of Muckcross (on carboniferous limestone) there has been much planting of exotic conifers and angiospermous shrubs from New Zealand, Australia, and South America. Near the Queen's Cottage *Prunus lusitanica* and *Rhododendron ponticum* have been planted and the *Rhododendron* has spread freely into the surrounding wood, replacing *Ilex*.

If the woods are natural in the sense that they are self-sown, this does not mean that there has been no interference in the past, or that there is none

now. As in so many oakwoods in Great Britain, oak seedlings are few, and there is a preponderance of old stems. Grazing by cattle, ponies and deer

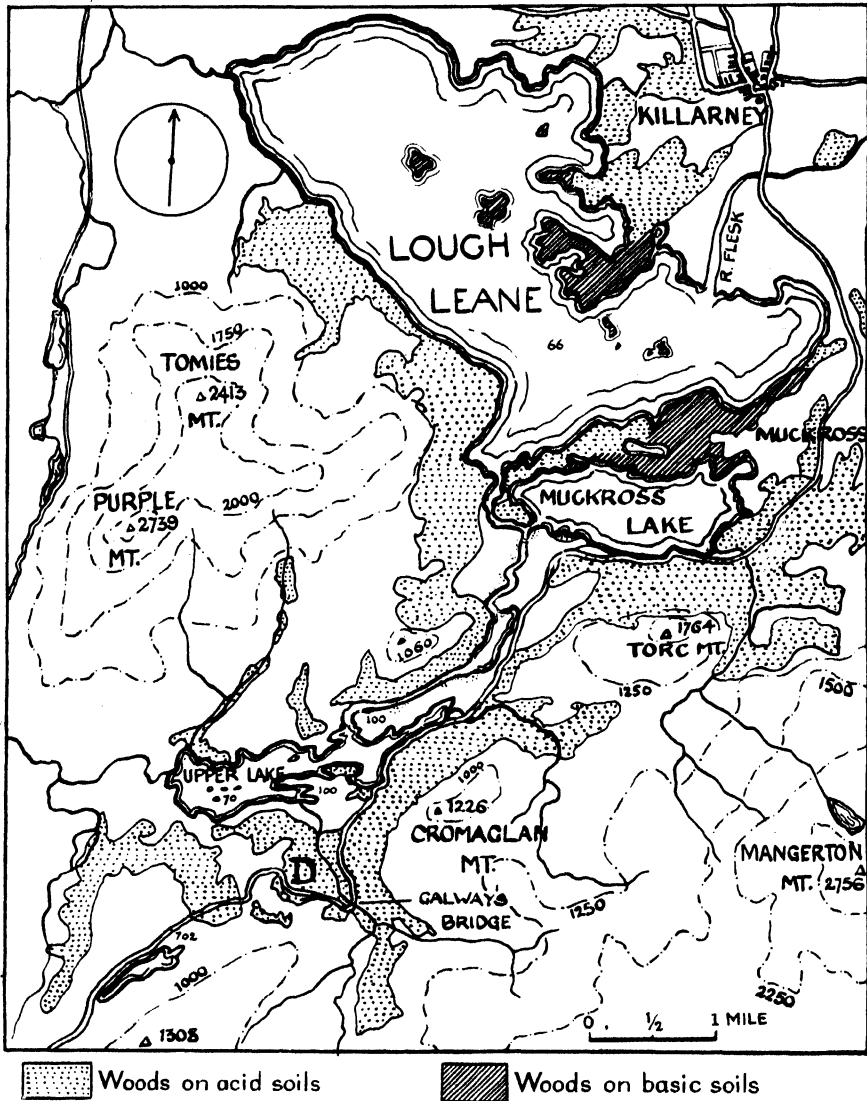


FIG. 1. Map of the Killarney region, taken from the 1 in. Ordnance Survey, showing the three lakes, the surrounding hills and the distribution of the natural and semi-natural woods on acid and basic soils. (D) gives the position of Derrycunihy wood. Heights in feet.

seems to be mainly responsible for this state of affairs and the conclusion that the upper limit of oak is climatic may well be questioned. Experimental evidence is needed to settle this point. Felling of older stems in the woods is

sporadic; some of it is legitimate, some not, and the relationship of the poacher towards the estate is strongly reminiscent of the state of affairs under the feudal régime in England. Now, as in the past, there is a good deal of timber lifting and poaching of deer. To get the deer easily, a refinement of cunning is practised which has important bearings on the vegetation. In places convenient to the poacher and most inconvenient to the keepers (usually near the lake), *Molinia* pasture is set on fire, as is the practice in the west of Scotland in sheep-grazing. The deer are attracted to the young and palatable grass and there shot. This burning is disastrous to invasion by woody plants, in particular to the thin-barked, fire-sensitive holly, whose blackened charred stems bear witness to the ravages of past fires and to the part it would play in undisturbed conditions. Deer are very frequent around the lake, and both the red deer (*Cervus elaphus*) and the Sika deer (*Cervus nippon*) are preserved; they remove the bark from the holly and graze the shoots. In winter they spend most of their time in the valley woods, where the holly is often lopped to provide them with winter food. Rabbits are scarce in the region, although the name Derrycunihiy means "wood of the rabbits".

We have no records of past exploitation which can be cited as precise evidence of interference in the oakwood at Derrycunihiy, where we worked. The most specific piece of evidence is the existence in this wood of a number of overgrown sites where charcoal was burned. Considerable samples from these hearths yielded charcoals which consisted largely of *Betula* and *Ilex*; several pieces of *Taxus* and one piece of *Quercus* were found, but no *Arbutus*. The discovery is a reminder of the days when the woods round Killarney were exploited for iron smelting, but we do not know to what extent the woods were felled or what species grew there and in what proportions.¹

From what we know of the history of Ireland, there seems little doubt that the Irish forests were formerly much more extensive than they are now. Much of the *Molinia* pasture, the *Calluna-Ulex* heath and at least some of the peat bogs are no doubt secondary, derived from woodland and maintained or extended by direct or indirect human interference. It is on the steeper slopes and the relatively inaccessible terraces, in places where drainage is good, that most of the oakwood survives.

The main part of this paper describes the structure of an oakwood (in its three varieties) growing on the southern slopes above the Upper Lake of Killarney. Time did not permit of an intensive study of the succession, but the work done demonstrated the existence of a holly scrub and some account of the succession is therefore given. Discussion follows on the ecological status of *Arbutus unedo*, and the relationships of the oakwoods to climate and to similar woods on the western seaboard of Europe.

¹ We are much indebted to Mr F. Jane, University College, London, for the determination of the charcoal.

CLIMATE

The nearest meteorological station yielding records over a long period is at Valencia (Cahirciveen), some 65 km. (40 miles) to the west of Killarney, and on the coast. We take these to be representative of the climate at Killarney, bearing in mind the moderating influence of the two arms of the sea (which reach within 24 km. (15 miles) of Killarney to the north and south) as well as the modifications produced by the high mountains round the lakes, which mitigate exposure and increase the orographic component of the rainfall. Since the meteorological data for Valencia were quoted in a recent issue of this *Journal* (Watt, 1936), there is no need to repeat them here and only a general summary is given.

Valencia has, for its latitude, the highest temperature in Europe; the annual mean is 10.45° C. and the range of the monthly means is only 8.1° C. The lowest monthly mean (January–February) is 6.9° C. and the highest (August), 15.0° C. The extremes show that frosts may occur from December to March, but they are rarely severe; Praeger (1934) records a frost damaging *Ulex* in Ireland. The mean annual rainfall is moderately high, 1414 mm. (56 in.), and although there is considerable variation throughout the year, the supply during the months with least rain (May, June) is ample—81 mm. (3.2 in.). This plentiful rain, much of it, as Praeger points out, in the form of a persistent drizzle, combined with the high relative humidity (the lowest monthly mean is 81 %), produces a damp climate, with a high N/S ratio (914). The number of hours of sunshine is higher than one might expect, but the maximum in May is still only 39 % of the possible; the minimum falls in December and January, with 16 %.

TOPOGRAPHY, GEOLOGY AND SOILS

The mountains round the Lakes of Killarney are formed of rocks of Lower Devonian age; they consist of superimposed beds of hard gritty Old Red Sandstone and softer slaty shale, which in Carboniferous times were thrown into folds along an east-west axis. As a result, the Upper Lake lies between steep but terraced slopes which are repeated in miniature on the small islands in the lake. At one time the rocks were overlain by beds of Carboniferous limestone, but this has been removed except in the deep trough of the fold at Muckross (Fig. 1); elsewhere the soils are formed from post-glacial débris from rocks of Lower Devonian age and the differences between the soil types appear to be bound up with the developmental stage reached in the geological process of smoothing out a broken topography.

Along the south and east shores of the Upper Lake, the alternating beds of sandstone and shale outcrop, and form a series of ageing slopes, the youngest consisting of steps or parallel terraces, the oldest of more gentle slopes. Each step in the terraced cliff is formed of the harder grits above and the softer

shales below, resting on the grit of the next terrace. The whole slope of the hills rising east of the Upper Lake thus consists of horizontal platforms of varying width, often about 6 m. (20 ft.), separated by vertical or almost vertical faces from 6–18 m. (20–60 ft.) high. Here and there streams tumble down the slopes, cutting deep and narrow gashes into the grit of the steps, and broader channels in the shale. The gritstone steps become undercut, the gashes widen and large angular blocks of resistant grit fall down the slope, to lie loosely on the alluvial fan of loamy soils derived from the shale; later these blocks become buried. With time the fan widens as the stream cuts its way back into the solid rock, and the slopes become more gentle and the soil more stable. At this stage the soil consists mainly of a fine loam derived from the slaty shale, with numerous angular boulders of grit and a few smaller stones of

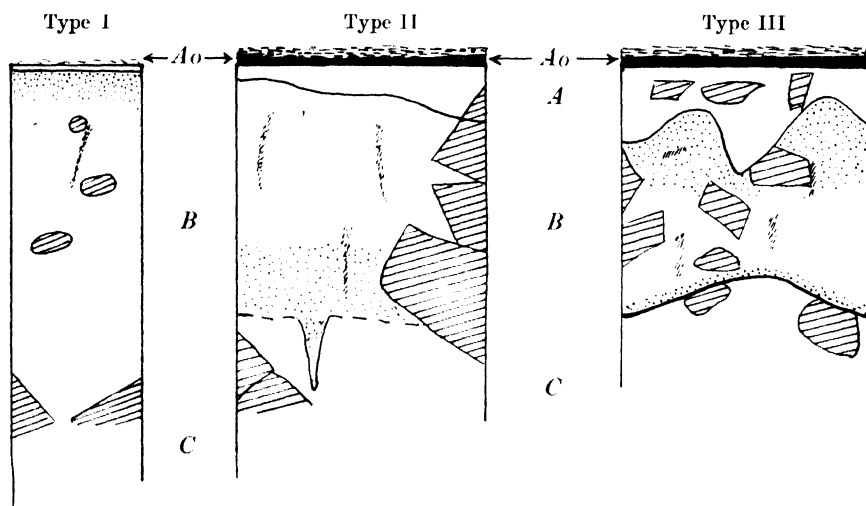


FIG. 2. Soil profiles of types I, II, and III, showing the differences in the development of the A_0 , A and B horizons. Boulders are obliquely shaded. The vertical bands are parts of reddish coloured "drainage channels". Bands of humus concentration in the mineral soil are stippled.

shale lying on or in it. No soil samples were collected from such early stages in the series of topographic changes, but the presence on such slopes (e.g. above Tower Lodge on Cromaglan mountain), of *Fraxinus excelsior*, *Ulmus montana* and *Fragaria vesca* suggests a fairly high base status. Soils of this origin, but older and slightly leached, are typical of the woodland described below as type I (p. 212) and they are dealt with here as "type I soils".

The gentler and more uniform slopes bearing woodlands and soils of type II appear to be much later stages in the maturation of the topography, although here and there a relatively broken terrace emerges, interrupting the uniform gradient of the slope. The angular boulders are here less numerous and conspicuous. Such stones and boulders are found in the ground to a depth of at least 4 ft. The gritty sandstone has weathered and contributes a larger share

to the soil itself, the sand being reinforced perhaps by washings from above. Geologically the soils bearing types II and III are similar.

The soils in the woodland are all podsolized, but to different extents. Large pits were dug in each of the major woodland types, and samples taken for analysis. The soil profiles fall into a series, from the slightly podsolized type I to the well-developed podsol of type III, which has an ill-developed iron pan at the base of the B horizon. The soil material of the A and B horizons at least are of post-glacial origin, consisting of angular boulders with soil packing and it is possible that in types II and III they lie directly on boulder clay. A comparison of the three soil profiles is made in fig. 2 and in Tables I and II.

Mechanical analysis of the separate horizons (Table II) confirms the view that these soils show three stages in development. In the C horizons there are high sand fractions (both coarse and fine sand), a relatively low clay content, and a medium though varying silt content. Movement of the clay is shown in types II and III. In type I there has been no movement, for the A and B₁ horizons contain the same high amount; in types II and III the low amounts in the A horizons are doubled and trebled respectively in the B horizons. In the B₂ horizons the clay content is much the same in all types, and double that found in the C horizon. The data for sesquioxides confirm the conclusion that types II and III are more intensively leached than type I.

The distribution of humus (see "loss on ignition") is interesting. In the slightly leached type I there is a decrease from above downwards; in types II and III there is an increase from A to B, and a decrease from B to C and the figures confirm the field observations, that in type II (Table I), there is more humus in B₂ than in B₁.

The pH profile (Table II (2)) is remarkably uniform in all three types. At the surface it ranges from 3.8 to 4.1, and even in the C horizon it is never above 5.8. All three soil types have a low base status. Type I is younger physiographically, and in soil development; types II and III are older and type III is more leached than type II.

Each of the three major soil types carries its own type of woodland. The differences in the soils appear to be largely due to geographical and geological causes and they probably largely determine the kind of woodland sere which develops on them. Differences in degree of podsolization may, however, be secondary, determined partly by the vegetational cover.

THE CLIMAX OAKWOOD, "QUERCETUM SESSILIFLORAE"

Derrycunihy Wood. The large oakwood called Derrycunihy (Fig. 3: Derrynaheirka on the 6 in. map, Ordnance Survey) was selected in 1935 on a preliminary visit, as a typical oakwood, suitable for detailed examination. It is approximately 0.5 sq. mile (130 ha.) in area, clothing a rough and uneven hillside. It is separated from the Upper Lake by a flat strip of *Molinietum*



Phot. 1. Derrycunihy Wood. *Molinietum* on alluvium in foreground

R. J. Lythgoe



Phot. 2. Type 1 woodland, Derrycunihy Wood, showing moss-covered live and dead stems of oak and moss-covered boulders. Hollies in the background and foreground.

J. S. Turner

Table I. *Comparison of soil profiles*

Horizon	Depth cm.	Type I Loose litter of partly decomposed oak and holly leaves and a thin layer of black, fairly compact <i>mor</i> , more friable and less soapy than in II and III. Much of the surface without moss cover	Depth cm.	Type II A soapy or greasy <i>mor</i> derived mainly from <i>Calluna</i> and <i>Vaccinium</i> , with occasional recognizable leaves of <i>Quercus</i> and <i>Ilex</i>	Depth cm.	Type III As in type II, mat of roots between A ₀ and A
A ₀	2-0				10-5-0	
A	0-2.5	Grey	0-5-23	Grey white, variable in depth, lower limit wavy. No marked A ₁ . Lowest band of A (2.5 cm.) is yellowish white	0-10-43	Variable in thickness. Grey white. Sharp transition from A ₀ to A and no clear A ₁ . Lowest 7.5-10 cm. yellowish
B	2.5-85	Ochre-yellow, fine friable loam, becoming lighter below. Enclaves of slaty shales disintegrated <i>in situ</i> ; strips of deeper ochre or red percolation channels	14-81	Upper part dark ochre, texture loamy. Lower part darker with more humus. Still darker pipes, with an A horizon down the centre of the upper part, descend to 113 cm. from the soil surface	26-88	Reddish yellow loam, lighter below. The lowest part 2.5-4 cm. thick, is darker, and resting directly on C is a thin layer of iron pan
C	85-	Coarser; greenish grey with a trace of yellow	81-	Bluish-grey-greenish; compacted	88-	Greenish grey, compact, coarse, gritty
		Throughout the profile, numerous stones of <i>shale</i> and a few of sand- stone		Throughout the profile, numerous angular boulders, all of sandstone		Throughout the profile, numerous angular boulders, all of sandstone

Table II

Horizon	Type I %	Type II %	Type III %
(1) Mechanical analysis of the soil horizons in types I, II, III			
A. Coarse sand	31.76	41.85	38.29
Fine sand	22.27	36.88	35.62
Silt	16.24	12.6	18.3
Clay	12.1	4.3	3.4
Sesquioxides	1.9	0.2	0.2
Loss on ignition	10.4	1.1	1.1
B ₁ . Coarse sand	27.2	35.0	23.7
Fine sand	27.8	30.8	23.2
Silt	16.3	9.1	16.7
Clay	12.2	7.2	11.4
Sesquioxides	3.6	4.7	5.3
Loss on ignition	7.6	7.7	9.5
B ₂ . Coarse sand	31.8	41.6	32.1
Fine sand	31.5	24.4	24.2
Silt	16.4	6.4	15.4
Clay	6.7	6.5	7.2
Sesquioxides	3.4	4.3	5.2
Loss on ignition	4.7	9.9	8.6
C. Coarse sand	41.1	51.7	51.5
Fine sand	34.3	31.1	26.6
Silt	14.75	9.0	10.1
Clay	3.2	3.3	3.5
Sesquioxides	0.9	0.8	1.8
Loss on ignition	2.5	1.8	2.6
(2) pH of the soils at different depths			
A ₀	4.1	3.9	3.8
A	3.8	4.1	4.0
B ₁	4.6	4.4	4.6
B ₂	4.7	4.4	4.6
C	5.7	5.7	5.8

about 18 m. (20 yd.) broad, and it rises to about 120 m. (400 ft.) o.d. A large stream cuts through one end of the wood, by the ruined "Queen's Cottage", and near this and the neighbouring gamekeeper's house there has been some felling and cultivation; *Fraxinus excelsior*, *Rhododendron ponticum* and *Prunus lusitanica* have been planted here. The greater part of the wood is very little visited, but an old path runs through the lower part, connecting the ancient villages near the Gap of Dunloe with a chapel at Galway's Bridge (Fig. 3); it is much trodden by the inhabitants and by tourists. Other paths in the wood are faintly marked and little used.

We have already discussed the question of man's interference in the Killarney oakwoods. In Derrycunihy there is specific evidence of former charcoal burning and present-day tree poaching. There may also have been some unsystematic felling by the owners, but all records of this are now lost. There are no timber lanes in the wood, and stumps of oak are rare, except near the main path.

The oakwood, even within this small area of Derrycunihy, is by no means uniform. Three main varieties are recognized and are called types I, II and III.

These, with their local modifications, are representative of the bulk of the oak-woods round Killarney.

Type I (Fig. 4) is striking and distinct. Tall, well-grown oaks and a well-marked second story of holly form a dense canopy over a field layer poor in species and thinly scattered over rocky ground (Pl. VI, phot. 3). There is no dwarf shrub layer. Bryophytes are particularly abundant on trees, logs and the numerous partly buried boulders (Pl. V, phot. 2). Type I is local; it grows

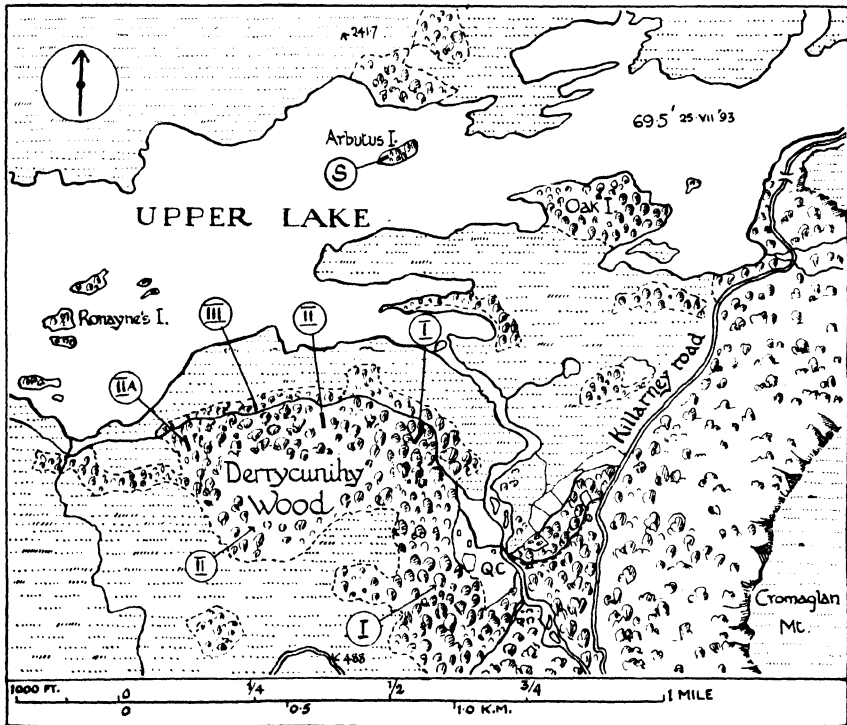


FIG. 3. Map of the Upper Lake, Arbutus Island and Derrycunihy wood, taken from the 6 in. Ordnance Survey, showing the Queen's Cottage (Q.C.) and the distribution of the woodland types. The sample plots (I, II, IIa, III, S) are shown as black rectangles, to scale.

on either steeply sloping or level ground and is easily recognized from a distance by the regularity of its rounded tree crowns. It is found in Derrycunihy mainly near the Queen's Cottage and also on Oak Island and in places on both sides of the road from Muckcross to Galway's Bridge.

Type II (Fig. 5; Pl. VI, phot. 4) is essentially similar to type I, with the same major species, but it differs in some well-marked features. The oaks are not so tall and vary more in size and form. *Sorbus aucuparia* and *Betula pubescens* are more frequent and *Ilex*, although more abundant than in type I, here forms

a discontinuous lower story. The canopy is more open, sunflecks larger and more frequent and there is a definite though discontinuous dwarf shrub layer of *Calluna* and *Vaccinium*. The field layer is sparse, though richer in species than in type I and these species are tall; some flower freely. Bryophytes are slightly less prominent on the ground but epiphytes are more luxuriant. The surface boulders are less in evidence, being partly covered by humus, partly hidden by the dwarf shrubs. Most of the woodland around the Upper Lake probably belongs to this type.

A part of Derrycunihy wood differing from type II in the form and number of the oaks and in the ill-developed shrub layer of *Ilex*, is regarded as an earlier stage in its development, and is called type IIa (Fig. 6; Pl. VI, phot. 5). It is marginal, and is possibly part of a secondary succession after fire or felling.

In type III (Fig. 7), which is on the whole more exposed, the oaks are still shorter, and they and *Sorbus* and *Betula*, which are both more frequent than in the other types, mingle their crowns with those of *Ilex*, which is here somewhat less frequent and smaller than in types I and II. The canopy is more open and the dwarf shrub layer more luxuriant, in particular the *Calluna*, which together with *Vaccinium* and *Pteridium* forms a tall and almost continuous cover (Pl. VI, phot. 6). This type is marginal at Derrycunihy, but variants of it occur locally on Cromaglan slopes and in the Galway valley, and it approximates to the oak-birch woodland near the altitudinal limit.

No sharp line demarcates these types. They were studied by making careful records (including drawings of the trees and shrubs) from representative sample plots. From these records Figs. 4-7 are drawn, and these diagrams represent accurately the structure of each type. The figures are supplemented by two tables. Table III supplies a complete list of the vascular flora of each type, with the frequencies of the species; Table IV adds further details which serve to differentiate the types.

Type I (sample plot I, Fig. 4). The sample plot of type I, 125 by 25 ft. (38 × 7.6 m.), was on ground sloping at 20° to the horizontal, facing roughly north-east and surrounded by woodland of its own type. The plants listed in Table III all occurred in the plot with the exception of *Betula* and *Taxus*, but these are included as being normal representatives of the type, though so rare as to escape inclusion in the plot.

Fig. 4 gives a clear picture of the structure of the wood, but fails to bring out all the characteristic features, some of which are better shown in photographs (Pl. VI, phot. 3, and Pl. V, phot. 2). These features are:

- (1) The uniform spacing of the large uniformly sized oaks.
- (2) The very obvious second story of *Ilex*.
- (3) The very dense shade cast by trees and shrubs. Even on a clear sunny day at noon, the woods are humid and sunflecks few and small.
- (4) The large mossy angular boulders scattered more or less uniformly over

the ground, and partly buried in it. These vary in size, some forming miniature cliffs up to 10 ft. (3 m.) high, most smaller, averaging 2-3 ft. (1 m.) across.

(5) The abundance of bryophytes covering most of the boulders and all but the topmost branches of the oaks with deep cushions.

(6) The absence of a dwarf shrub layer and the very poorly developed field layer of non-flowering species.

Table III. *Comparison of the floras in types I-III*

Name	Type I	Type II	Type IIa	Type III
Species occurring in all four types				
<i>Quercus sessiliflora</i>	d.	d.	d.	c.d.
<i>Ilex aquifolium</i>	d.	d.	d.	c.d.
<i>Sorbus aucuparia</i>	r.	o.	o.	f.
<i>Betula pubescens</i>	v.r.	r.	o.	f.
<i>Taxus baccata</i>	r.	r.	v.r.	—
<i>Arbutus unedo</i>	—	—	—	r., local
<i>Vaccinium myrtillus</i>	f.	a.	a.	a.
<i>Luzula silvatica</i>	f.	a.	a.	a.
<i>Hedera helix</i>	o.	o.	o.	a.-f.
<i>Lonicera periclymenum</i>	o.	o.	o.	a.-f.
<i>Oxalis acetosella</i>	f.	o.-r.	a.	f.
<i>Blechnum spicant</i>	f.-o.	a.	a.	a.
<i>Dryopteris aemula</i>	f.	f.	f.	o.
<i>Pteridium aquilinum</i>	f.-o.	o.	f.	a.
<i>Hymenophyllum peltatum</i>	(ep.)	f.(ep.)	l.	o.
<i>Hymenophyllum tunbridgense</i>	f.	f.	l.	f.
Species occurring in three types only				
<i>Molinia coerulea</i>	—	r.	o.	r.
<i>Polypodium vulgare</i>	f.	o.-r.	—	o.
Species occurring in two types				
<i>Calluna vulgaris</i>	—	a.	—	a.
<i>Dryopteris dilatata</i>	—	r.	—	r.
<i>Dryopteris filix-mas</i>	—	r.	r.	—
<i>Agrostis tenuis</i>	r.	—	f.	—
<i>Viola sylvatica</i> agg.	—	—	r.	r.
<i>Potentilla erecta</i>	—	—	f.	o.
Species in one type only				
<i>Agrostis stolonifera</i>	—	—	r.	—
<i>Euphorbia hiberna</i>	—	—	f.	—
<i>Carex remota</i>	—	—	o.	—
<i>Asplenium adiantum-nigrum</i>	—	—	r.	—
<i>Galium saxatile</i>	—	r.	—	—
<i>Saxifraga spathularis</i>	—	—	—	o.
<i>Hypericum pulchrum</i>	—	—	—	r.
<i>Solidago virgaurea</i>	—	—	—	r.
<i>Deschampsia flexuosa</i>	—	—	—	o.
<i>Rhododendron ponticum</i>	—	—	—	1 seedling
<i>Viola palustris</i>	—	—	—	v.r.
<i>Hypericum androsaemum</i>	—	—	—	v.r.

The oaks, all *Quercus sessiliflora*, are mature, rather overmature in a forester's eyes, between 150 and 200 years old (counts were made on old stumps), and between 50 ft. (15 m.) and 70 ft. (21 m.) high. They are the tallest trees in the Killarney woods. They are widely and rather uniformly spaced, of fairly uniform height and almost all have a stem free from large branches to a height of at least 10 ft. (3 m.) and a large spreading crown

(Fig. 4). In the small area of the sample plot the trees happened to be closely similar, the girths at breast height being between 7 and 8 ft. (2.3–2.6 m.), but measurements in Derrycunihy in areas taken to be type I, or approximating to it, show that the trees vary in girth from 3.0 to 9 ft. (92–275 cm.) with a mode at 6½ ft. (198 cm.) (Fig. 8). There is, however, a striking absence of small trees and saplings. The density, calculated from the rather small area of the

Table IV. *Comparison of the woodland types*

	Type I	Type II	Type III
<i>Quercus sessiliflora</i> :			
No. trees per acre (ha.)	35 (86)	85 (209)	280 (687)
Girth at breast height: Range	3–9 ft. (92–275 cm.)	1¼–7½ ft. (38–222 cm.)	7 in.–2 ft. 10 in. (18–85 cm.)
Mode	6½ ft. (198 cm.)	3½ ft. (107 cm.)	Prox. 1 ft. 6 in. (45 cm.)
Height of trees: Max.	70 ft. (21.3 m.)	50 ft. (15.2 m.)	25 ft. (7.6 m.)
Mean	60 ft. (18.3 m.)	45 ft. (13.7 m.)	17 ft. (5.2 m.)
<i>Ilex aquifolium</i> :			
No. shoots per acre (ha.)	875 (2140)	940 (2310)	700 (1720)
Height of shoots: Max.	30 ft. (9.1 m.)	25 ft. (7.6 m.)	19 ft. (5.8 m.)
Mean	14 ft. (4.3 m.)	12½ ft. (3.8 m.)	11½ ft. (3.5 m.)
<i>Vaccinium myrtillus</i> :			
Height of shoots: Max.	30 cm.	100 cm.	100 cm.
Mean	10–20 cm.	60–70 cm.	46–60 cm.
<i>Calluna vulgaris</i> :			
Height of shoots: Max.	Abs.	210 cm.	150 cm.
Mean	—	100 cm.	90–120 cm.
Dwarf shrub and field layer	Poor, open, round boulders	Locally closed	Closed, dense, tall
No. species vascular plant in dwarf shrub and field layer	12	16	22
Illumination of field layer (arbitrary units)*	6.8	8.7	26
<i>Hymenophyllum peltatum</i>	Only on oak above 30 ft. (9.1 m.)	On oak to within 3 ft. (1 m.) of ground	On oak to within 3 ft. (1 m.) and on rocks
Bryophytes, Associules	Both open and closed	More closed than open	Mostly open
Soil type	Loamy, only slightly leached	Loamy sand, leached	Loamy sand, leached, with pan
Clay fraction in A horizon	12.1	4.3	3.4

* These figures are worked out from observations of light intensities taken with a photoelectric cell, combined with estimations of the number and intensity of sun spots. The method will be described in a paper by G. C. Evans.

plot, is low—approximately thirty-five stems to the acre (eighty-six to 1 ha.). The oaks form an almost closed canopy although their main branches are relatively spindly and bear no very heavy masses of foliage. A characteristic feature is the abundance of epiphytes—mosses, liverworts and ferns—which clothe the main branches and parts of the trunks of the oaks to a height of at least 50 ft. (15 m.). On the ground dead twigs, branches and large boughs of oak are frequent, although they appear to rot away very rapidly.

Oak seedlings of one or two years' growth are rare, and they grow mainly in clearings or near the paths. No plants intermediate between these and mature trees of at least 2 ft. (60 cm.) girth were discovered, even in gaps left by large dead, fallen or felled trees.

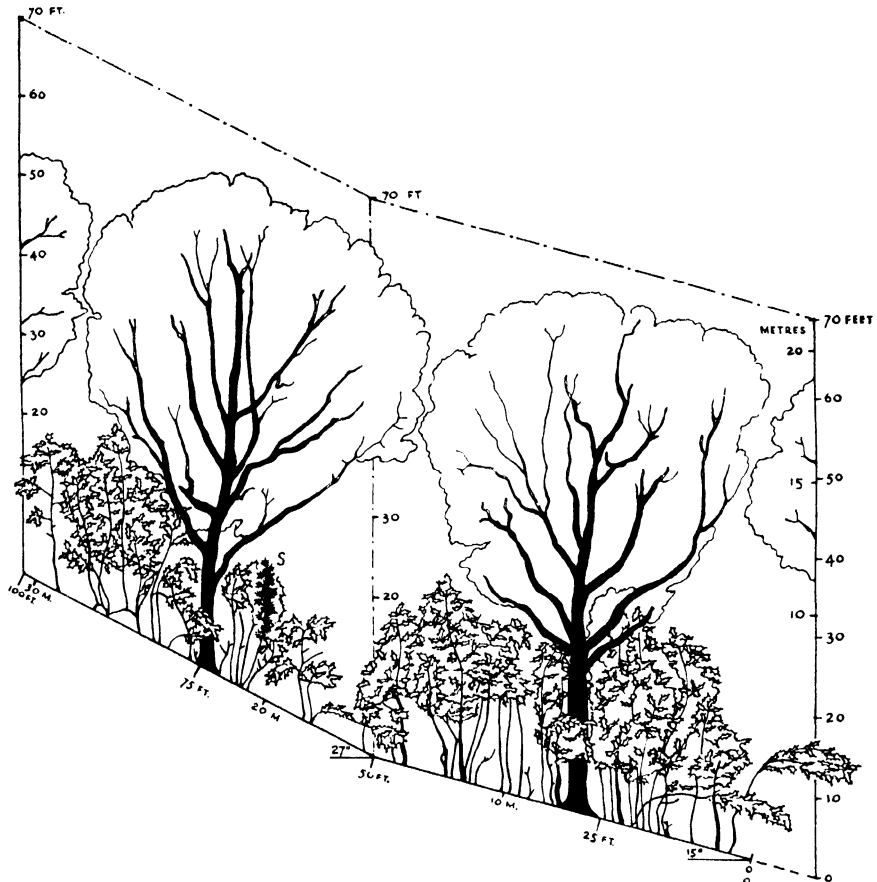


FIG. 4. Type I woodland; profile diagram to scale of part of sample plot I, which is 25 ft. (7.6 m.) wide. All trees and shrubs drawn and measured on the plot; boulders and field layer omitted. The large trees are *Quercus*, the others are *Ilex*, except (S), *Sorbus*. (Note. In this, and Figs. 5, 6, 7, 9, I am indebted to Mrs M. Tomlinson who kindly modified the diagrammatic representation of the smaller trees and shrubs and thus made my coloured diagrams suitable for reproduction in black and white.—J. S. T.)

Other trees are rare, *Sorbus aucuparia* and *Betula pubescens* growing only where the canopy of oak is slightly less dense than usual. Seedlings of both are occasional. *Taxus baccata* is more common here than in the other types and it is scattered thinly over the area, probably less than one tree to 2 acres (0.8 ha.). These yews are all large, old trees, about 50 ft. (15 m.) high, with abundant epiphytes and thinly clad with relatively short-lived leaves. Seedlings up to

3 cm. high are much more frequent than those of the oak, and they appear to grow well, but saplings are absent.

Beneath the oaks is a well-defined layer of *Ilex aquifolium*, which is the only shrub. These are mostly large, well grown, with a maximum height of 30 ft. (9 m.) and often with many adventitious shoots and suckers. Many have a perfect pyramidal form but shrubs with a peculiar flat top are also common. In these, the topmost branches are produced in a whorl at 90° to the main stem. It is possible that this form and the frequent growth from the base are the result of lopping the young trees to provide the deer with winter food. Small seedlings of *Ilex* and young plants are frequent. The stems of the *Ilex* are, on the whole, free from dense mats of bryophytes and large lichens, as one might expect for young trees with a smooth bark.

The field layer is poor in species (12) and scanty. If we omit the *Hymenophyllums*, which are best treated with the bryophytes, there are ten species of vascular plants in the type. Of these, *Polypodium vulgare* is an epiphyte and rarely found on rocks, *Lonicera* and *Hedera* are occasional as lianes on oak and holly. The other plants (Table III) grow on the ground, rooted mainly round the bases of boulders forming an open layer. Between the boulders the ground is largely free of plants, with a light leaf litter. None of the vascular plants was in flower or fruit (August), but all possess means of vegetative propagation. The *Vaccinium* grows to a foot in height, but does not form bushes, and the shoots are straggling, and the leaves few and small. Seedlings of *Vaccinium*, *Hedera* and *Lonicera* are occasional, the seeds presumably coming from plants flowering in neighbouring clearings, paths or other woodland types where the canopy is less dense.

No less striking than the poverty of the field layer is the great abundance of the bryophytes. In the sample plot of type I there are twenty-three species of moss and twenty-nine of liverworts. They form well-defined communities which are described on p. 221.

Large areas of type I near the Queen's Cottage, on both sides of the stream, have been invaded by *Rhododendron ponticum*. This plant was introduced to the district, probably sixty years ago; it flowers and fruits readily in the open and has spread naturally from the drives and gardens. Once established in the woods it increases by the rooting of branch tips (cf. *Viburnum opulus* at Wicken fen, Godwin, 1936) and a very dense layer of bushes is formed. It grows to a height of 30 ft. (9 m.) and competes successfully with all but the largest holly trees. As a result, the woodland is changed markedly in appearance. The *Ilex* story is replaced by an even denser one of *Rhododendron* and the shade increases. Very few higher plants survive in the field layer (e.g. *Vaccinium myrtillus* and *Oxalis acetosella* are rare), and there is a very marked reduction in the number of bryophytes and the thickness of the mossy cushions on the boulders. Seedlings of *Rhododendron* are occasionally found far from the parent bushes, but so far invasion of the Killarney woods is mostly marginal.

Type II (sample plot II, Fig. 5). This type is much more variable than I and is therefore more difficult to describe in precise terms. It is probably modified to some extent by sporadic felling of individual trees and it is locally modified by aspect and drainage. The sample plot was 100 by 25 ft. (30.4×7.6 m.) on a north-facing slope. The bulk of Derrycunihy wood is made up of type II and its variants.

The oak is again the dominant tree, but it reaches a height of only 45–50 ft. (13.7 – 15.2 m.). The trees are more variable in size, and range in girth from

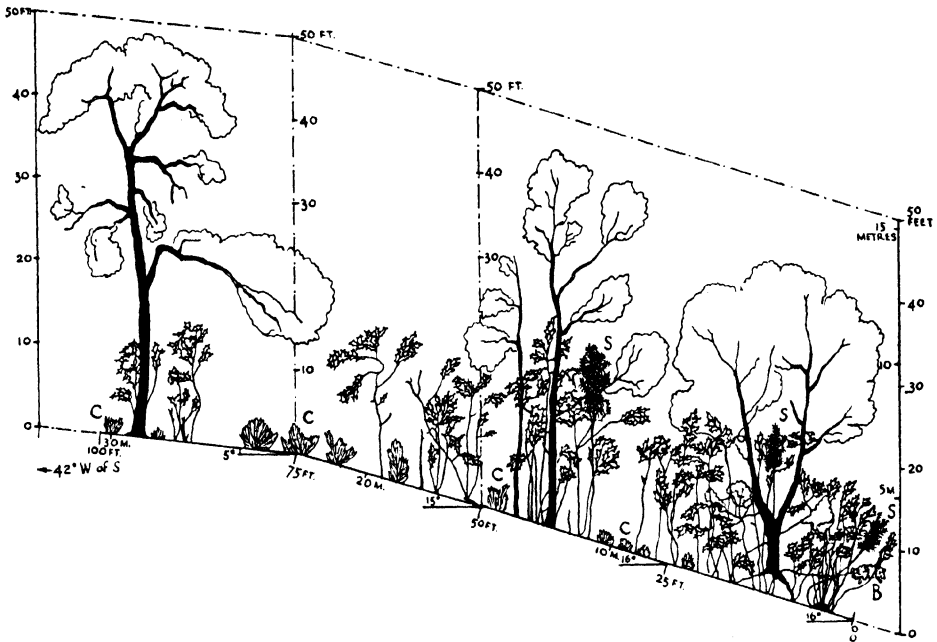


FIG. 5. Type II woodland; profile diagram to scale of plot II, 25 ft. (7.6 m.) wide. Boulders and field layer omitted. (S) *Sorbus*, (B) *Betula*, (C) *Calluna*; the other shrubs are *Ilex* and the trees *Quercus*.

1 ft. 3 in. to 7 ft. 4 in. (38–222 cm.), with a mode at $3\frac{1}{2}$ ft. (107 cm.) (Fig. 8). In form they vary from trees with heavily branched wide-spreading crowns to those with straighter main stems and smaller crowns. Typical F_1 and F_2 trees are present (Watt, 1924). The occasional seedling oaks and scattered small trees suggest that regeneration is adequate in this type. *Sorbus* and *Betula* are both more frequent than in type I and *Betula* is no longer restricted to clearings. These two species range in height from 15 to 25 ft. (4.6–7.6 m.); their crowns are narrow and they cast little shade. *Taxus* is rare, and there is no *Arbutus*. Seedlings of *Sorbus* are frequent and one seedling *Rhododendron* was found; it is about half a mile distant from the nearest bush.

Though more numerous per unit area than in type I, the holly is smaller, with smaller crowns and more varied stem diameter; a few only are large with pyramidal crowns. Seedlings are occasional.

The crowns of the oak do not everywhere close overhead, nor does the holly form a continuous subcanopy. The result is that sunflecks are frequent on the ground, and locally there are large sunlit patches. Correlated with this greater light intensity, the dwarf shrub layer is well developed, consisting of tall (60–70 cm.) vigorous *Vaccinium myrtillus*, which in places forms a continuous layer and sometimes flowers. Under a more open canopy it is accompanied by *Calluna vulgaris* (absent from type I), which may share dominance with it.

The most notable features of the field layer are the greater frequency of *Blechnum spicant*, the greater vigour and frequency of *Luzula silvatica*, which, however, still shows the same diffuse growth form and absence of flowers, and the reduced frequency of *Oxalis acetosella* and *Polypodium vulgare*. In addition a few species occur which are not found in type I, viz. *Molinia coerulea*, *Dryopteris dilatata*, *D. filix-mas* and *Galium saxatile*, all of which are rare.

Type IIa (Fig. 6; Pl. VI, phot. 5). This subtype is easily recognizable by the form of the oak trees, which are numerous, straight and thin-stemmed, bearing small crowns. It is the only woodland type in Derrycunihy where one obtains an immediate and strong impression of an immature wood. There are about 200 oak stems to the acre (500 per ha.)—many more than in type II, and few large trees, most of which are of the F_2 or F_3 form. They reach a maximum height of 45 ft. (13.7 m.), with a mean of 35 ft. (10.6 m.). The distribution curve for the tree girths resembles closely that of II, but there are fewer large trees and more saplings (Fig. 8). The canopy is more open than that of II, and more uniform, as the trees are evenly spaced.

A fairly large area of this subtype occurs in Derrycunihy, marginal to type II and abutting on the *Molinia* marsh at one end of the wood. It occurs on sloping ground, with fewer boulders and irregularities than in the other types, and the youngest stages of IIa run out on spurs into the marsh, at right angles to the inclination of the ground; it is bounded on the edge of the marsh by a very narrow transitional zone of small oaks with *Arbutus*, resembling type III. Walking along a contour from the marsh inwards, one passes gradually from type IIa to II. It is supposed that IIa represents a stage in the development to II, possibly following wholesale felling or fire.

Sorbus and *Betula* are both rather more frequent in IIa than in I or II and they have the same form as the oaks and on the whole are as tall as these. *Taxus* and *Arbutus* are absent. *Ilex* is still abundant, but the trees are scattered and no longer form the very well-marked second story which is found in both I and II. There are only 200 stems of holly to the acre (as against 870 in I, 940 in II and 700 in III). The lack of the dense holly layer contributes materially to the lightness of the wood.

Seedlings of *Sorbus* (a.), *Ilex* (f.), *Quercus* (o.), and *Hedera* (o.) are all present.

The dwarf shrub layer corresponds closely to that of type II, but *Calluna* is absent. The layer is not entirely closed, but over large areas *Vaccinium* forms a closed layer of healthy bushes, at most a foot high, locally very dense and rarely fruiting. In the field layer the chief species are the same as in type II. *Oxalis* is, however, more abundant and some species are found which do not occur in types I or II: *Asplenium adiantum-nigrum*, *Agrostis stolonifera*,

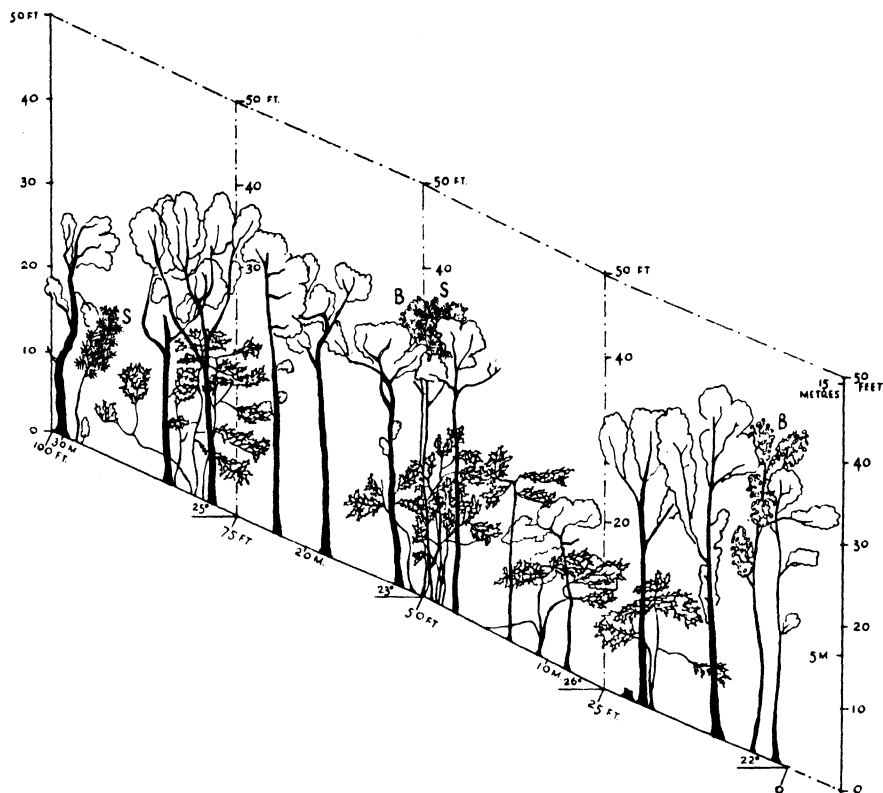


FIG. 6. Type IIa woodland; profile diagram to scale of plot IIa, 25 ft. (7.6 m.) wide. Symbols as in Fig. 5.

Agrostis tenuis, *Viola sylvatica* (agg.), *Potentilla erecta*, *Euphorbia hiberna* and *Carex remota*. The last six of these are also found in large clearings within types I and II, and their presence in IIa may be correlated with the paucity of *Ilex* and greater light intensity, rather than with specific soil differences. We have no precise data on the soil profile of IIa.

The bryophytes were not investigated in detail in this plot, but it seems probable that they do not ascend the trees to the same heights as in types I

and II. The other common epiphyte, *Polypodium*, was not recorded. Both species of *Hymenophyllum* are less frequent than in the darker woods.

Type III (sample plot III, Fig. 7). The small sample plot of type III (75 × 25 ft., 22·8 × 7·6 m.), lying between the path and the *Molinietum* at the edge of the wood, is on very rough ground; the upper part is strewn with large moss clad boulders of sandstone, the lower part is steeper, with smaller boulders.

The wood is mixed, with *Quercus*, *Ilex*, *Betula*, *Sorbus* and rare *Arbutus*. Although the oak trees are more abundant than in the other types, they are not dominant. Their average height is only 17 ft. (5·2 m.), their maximum 25 ft. (7·6 m.), and with the other trees they form a single layer. The oaks which are only slightly taller than the hollies, cast little shade; they are stunted and twisted and vary greatly in girth (7 in. to 2 ft. 10 in.)¹. *Betula*

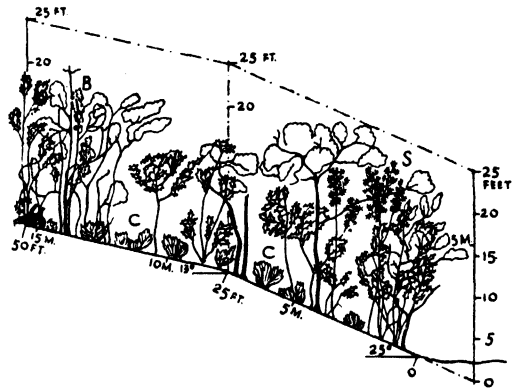


FIG. 7. Type III woodland; profile diagram to scale of plot III, 25 ft. (7·6 m.) wide. Boulders and field layer omitted. Symbols as in Figs. 4-6.

and *Sorbus* are frequent, *Ilex* stems are more frequent than in I or II, although the trees have smaller crowns. Seedlings of *Sorbus* (a.), *Ilex* (o.), *Taxus* (l.), *Quercus* (l.) and *Crataegus monogyna* (l.) occur. *Arbutus* is rare, and neither the tree nor its seedlings were found in the plot. One large tree near the plot, though fallen, had produced many upright shoots rising to 20 ft. (6 m.) and it was apparently holding its own in the surrounding canopy of oaks and hollies. There is little doubt that such *Arbutus* trees are survivals from the early stages in the sere (p. 229).

There are many sunflecks and large gaps in the canopy and the subsidiary vegetation is richer in species than in types I and II, though the three types share most of the common species (Table III). *Vaccinium* grows vigorously, averaging 1½-2 ft. (46-60 cm.) high and occasionally sets ripe fruit. *Calluna* is abundant and almost shrub-like; it forms large bushes, mostly about 3 or

i The frequency curve (Fig. 8) for this type is based on only twelve trees.



J. S. Turner

Phot. 3. Type 1 woodland, Derrycunihy Wood, showing the top story of *Quercus sessiliflora*, the middle story of *Ilex aquifolium* and the moss-covered boulders. There is little herbaceous vegetation.



J. S. Turner

Phot. 4. Type 2, Derrycunihy Wood, showing the luxuriant dwarf shrub layer of *Calluna* and *Vaccinium* under an uneven canopy of oak and holly.



J. S. Turner

Phot. 5. Type 2a, Derrycunihy Wood, showing oaks of more uniform size. The dwarf shrub layer is mainly of *Vaccinium*. *Euphorbia hiberna* in the foreground.



J. S. Turner

Phot. 6. Type 3, Derrycunihy Wood, Holly and stunted oak form an open canopy over an undergrowth mainly of *Calluna* (in flower) *Vaccinium* and *Pteridium*.

4 ft. (0.9–1.2 m.) high, but reaching 5 ft. (1.5 m.), and flowering freely. Some of the bushes are grazed slightly by deer or perhaps hares, and a few have dead shoots.

Pteridium is also frequent, its fronds widely spaced and 2–3 ft. (0.6–0.9 m.) high. *Luzula silvatica* occurs in the form common to all these woods—i.e. with diffuse shoots arising from long creeping rhizomes with no flowers or fruits. *Molinia*, *Erica cinerea* and *Deschampsia flexuosa* are all local and commonest near the margin of the wood. Seedlings of *Calluna vulgaris*, *Vaccinium myrtillus* and *Potentilla erecta* are all occasional.

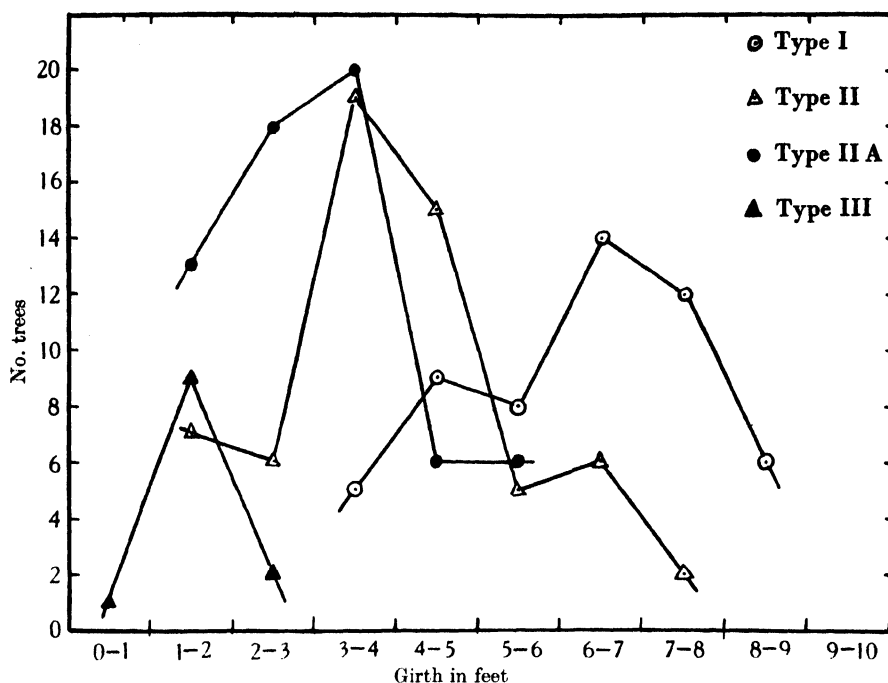


FIG. 8. Frequency distribution curves for tree girths (*Quercus*) in the four woodland types. Girths measured at breast height on trees of or near the sample plots. Type I, 54 trees; Type II, 60 trees, Type IIa, 63 trees, Type III, 12 trees only.

Bryophytes are less obvious than in the other types, and the trees are freer of them. The epiphytes, *Polypodium vulgare* and *Hymenophyllum peltatum*, occur only on the bases of the trees, or on the ground.

THE BRYOPHYTIC COMMUNITIES OF THE OAKWOODS

The ecology of the bryophytes was studied in great detail by Dr P. W. Richards, who has been good enough to allow us to summarize his main conclusions. This has inevitably led to over-simplification of the facts; but we have presented the data here in order to give a well-balanced picture of the woods. A full treatment of the bryophyte ecology is given by Richards (1938).

The Killarney district has one of the richest bryophyte floras in Europe and many rare "Atlantic" and subtropical species as well as a few British endemics are found. Some of these are widespread, others are found only in sheltered glens, as at Torc. The woods are rich in both species and individuals, and in some places they form such thick carpets on the boulders and trees as to suggest a comparison of these woods with the Malayan "Moss" forests.

In the Derrycunihy woodland types there are about forty species of mosses and fifty of liverworts, and these are distributed in well-marked micro-communities. Seven different habitats are recognized, five with a similar micro-climate, and in each are found open and closed communities showing succession towards a climax. In the three woodland types at Derrycunihy the following communities are described; we give only the dominant or characteristic species:

(1) *The closed boulder associule.* This is a dense sward of tall species, mostly orthotropic mosses. *Hylocomium brevirostre*, *Rhytidiadelphus loreus* and *Thuidium tamariscinum* are co-dominant; *Dicranum majus*, *Plagiothecium undulatum* and *Polytrichum formosum* are abundant and constant and the fern *Hymenophyllum tunbridgense* (similar in life form to the bryophytes) is frequent.

(2) *The open boulder associule.* This is the early stage of the serule leading to (1). It consists largely of foliose hepatics and plagiotropic mosses. No one species is very abundant, but in type I, *Diplophyllum albicans*, *Heterocladium heteropterum* and *Sematophyllum micans* are the most frequent species.

(3) *Associules on logs and fallen branches.* The climax in this habitat is a sward differing from that of the closed boulder community mainly in the presence of *Isoetecium myosuroides* as a common species and the rarity of *Polytrichum formosum*. The open community on logs is quite different from that on boulders in the early stage of the succession, *Cephalozia catenulata* and *Nowellia curvifolia* being characteristic colonizers of fallen branches after the death of the original epiphytes. Later on a climax associule very similar to the closed boulder associule develops.

(4) *Associule on tree bases (up to 3-6 ft.).* This community, occupying the lowest of the three epiphytic zones, resembles that on logs, although a few exclusively epiphytic mosses (e.g. *Isoetecium myurum*) enter into its composition. *Peltigera canina* is the only common lichen.

(5) *Associule on trunks above 3-6 ft. and on large branches.* The climax community here is dominated by *Isoetecium myosuroides*, which forms thick, almost continuous carpets. On the larger horizontal branches mats up to 6 in. thick occur, and amongst the dominant, *Plagiochila punctata*, *P. spinulosa* and *Hymenophyllum peltatum* are abundant. These mats, when old, are sometimes colonized by species of the closed boulder associule (e.g. *Thuidium tamariscinum*) which are not usually present as epiphytes. On the lower surfaces of horizontal or sloping branches, the bryophyte community is

replaced by "leprose" lichens, with occasional bryophytes such as *Metzgeria furcata*.

(6) *Associule on twigs and smaller branches.* The uppermost zone of epiphytes ascends to the tree tops, and the community, which is never completely closed, is dominated by *Ulota crispa* and *Frullania tamarisci* accompanied by *Frullania germana*, *Drepanolejeunea hamatifolia*, etc. Lichens are frequent in this zone and on the uppermost twigs they are often the only epiphytes.

Most of the epiphytes are found on the oaks, but the same communities occur on *Ilex*, though they are there less well developed, possibly owing to the smoother bark and thinner, younger trunks of these trees. In types II and III numerous epiphytic bryophytes occur on *Calluna* and *Vaccinium* and a zonation of communities is distinguishable on the taller bushes.

As far as the bryophytes are concerned the three types of wood at Derry-cunihy are major habitats forming a series: type I is constantly dark and humid, with tall trees and little undergrowth, types II and III have smaller trees and in them the light and wind can penetrate more easily to the ground; there is also a more fluctuating and probably a greater saturation deficit, and more competition by the low growing vascular plants. As far as the number of species in the plots go, there is little difference in the bryophytes in the three types, as shown in Table V.

Table V

Community	Number of bryophytes in the communities		
	Type I	Type II	Type III
Open boulder	30	28	25
Closed boulder	30	30	32
Logs	17	No logs	5
Base of oaks	7	7	14
Middle of oaks	9	10	14
Twigs and small branches of oaks	11	7	10

As we pass, however, from types I to III, the open boulder community occupies progressively less area, and in III it is fragmentary. The closed boulder community is similar in all three types, but the species differ somewhat from type to type. For instance, *Heterocladium heteropterum*, var. *fallax* is found only in type I, and *Hylocomium splendens* (presumably a light lover) is rare in I, occasional to locally frequent in II and frequent to abundant in III. In type III the dense shade cast by dead leaves tangled in the bases of *Calluna* bushes often excludes mosses altogether.

One of the most striking differences between the types of wood is the tendency for the three epiphytic communities to move downward as one passes from I to III. Species which occur in the oak crowns in I grow lower in II and descend almost or quite to the ground in III. Moreover, the species of the upper zones tend to become mixed with those of the zone below so that the differentiation of the communities is less sharp in III. The interest of this

"descent" of the epiphytes lies in the fact that an exactly parallel phenomenon has been noted with epiphytic flowering plants in the tropical rain forest. In types of rain forest where the light intensity in the undergrowth is very low the epiphytes are mostly confined to the tree tops, but in better illuminated types they descend to much lower levels (Davis & Richards, 1933) and it has previously also been noted for bryophytes on trees in Argyll by N. M. Martin (1938). At Killarney it was shown by the bryophytes and by *Polypodium vulgare* and most clearly of all by *Hymenophyllum peltatum*. The other common filmy fern, *H. tunbridgense*, occurs mainly on the ground, but *H. peltatum* is found on oaks above about 30 ft. (9.1 m.) from the ground in type I; in types II and III it comes to within 3 ft. (1 m.) of the ground, and in type III it is found even on boulders. Somewhat the same behaviour is also shown by the saprophytic fungus, *Polystictus versicolor*; in the open it grows on logs on the ground; in type III it grows on logs near the ground and in type I it was found only on the uppermost dead branches of the trees.

Lichens are frequent in the woods, but they are not found in the boulder communities, and are only abundant on the upper branches of the trees. "Leprose" lichens occur in abundance on the holly trunks and on the under sides of oak boughs. Richards noted thirteen species from the sample plots but in the neighbourhood Mrs L. Porter, who joined the party for a few days, listed ten species on the upper boughs of trees, thirty-three species on smaller branches and trunks, and twenty-nine on rocks. Very few of the last are represented in the woodland itself, as the rocks are largely occupied by the bryophyte communities.

THE SUCCESSION

The woods described as types I, II, III are found on three different types of soil, all derived from Lower Devonian sandstone and shale. We are not inclined to regard them as serally related to one another, but we leave the matter open for the time being. The study of developmental succession is rendered extremely difficult by the disturbances caused by grazing, burning and past exploitation, and by the varied topography. Type IIa certainly appears to be a seral stage leading to type II, but elsewhere successional relationships are more obscure. On less accessible places, on Cromaglan mountain side and in particular on the islands, we believe that we can distinguish young stages in priseres and these will now be dealt with.

Reference has already been made (p. 206) to the physiographic stages leading to soils of type I. Such stages exist on the steeper slopes of Cromaglan mountain, above Tower Lodge. Here the weathered and eroded products of the shaly beds predominate and form a steeply inclined fan of loamy soil in and on which lie the large angular boulders of grit. The woods on such young soils are in an early stage of development, presumably to type I woodland. The soil in these woods is unleached and largely devoid of humus; it bears a relatively rich flora, forty-six species being listed during a rapid ascent of the steep

slope. In a young stage *Quercus sessiliflora* is not yet dominant; *Ilex* is the most abundant woody plant and with it occur *Fraxinus excelsior*, *Betula pubescens*, *Taxus baccata* and *Corylus avellana*. In a later stage, *Quercus* dominates, but *Fraxinus* and *Ulmus montana* are occasional. The subsidiary vegetation in both stages suggests immaturity; it is a heterogeneous mixture of plants which do not form a closed layer: *Agrostis tenuis* (l.a.), *Blechnum spicant* (f.-l.a.), *Calluna vulgaris* (o.-f.), *Vaccinium myrtillus* (f.), *Aira caryophyllea* (l.), *Saxifraga spathularis* (f.), *Digitalis purpurea* (l.), *Luzula silvatica* (l.f.), *Cirsium palustre* (l.), *Anthoxanthum odoratum* (o.), *Hypericum pulchrum* (o.), *Deschampsia flexuosa* (r.), *Lysimachia nemorum* (l.f.), and *Fragaria vesca*.

An entirely different type of succession was distinguished on the islands in the Upper Lake. Here the bare rock is colonized by heath plants, and the heath is invaded by a holly scrub, which in turn is replaced by woodland. We are not clear as to the final woodland type which would become established in such places; woodland on the islands at present resembles type III of the mainland, but we cannot be sure that it is a climax. It is considered worth while describing the sere on Arbutus Island, however, especially as *Arbutus*, a characteristic Lusitanian species, plays a part in it.

The islands are generally markedly convex, with steep sides and rounded summits. On the lower slopes there is usually bare rock, with *Molinia* and *Calluna*, the chief species established in the cracks. Higher up there is a well-marked belt of heath with *Calluna* and *Ulex gallii* co-dominant, *U. europaeus* locally dominant and *Erica cinerea* locally abundant. In this heath are scattered bushes of holly, *Arbutus* and *Sorbus*. It gives way to a holly scrub in which *Arbutus* and *Taxus* persist. Finally, on some islands, the climax or subclimax is reached with *Quercus sessiliflora* dominating.

Of the time spent in studying succession the greater part was occupied in making a belt transect through the successional stages on Arbutus Island (Fig. 3). This island is one of the largest of the dozen in the Upper Lake. It is approximately 130 yd. (120 m.) long and 45 yd. (41 m.) broad, the long axis lying roughly north-east to south-west. The nearest mainland is 110 yd. (100 m.) north, separated by deep water. The island is built of an outcrop of sandstone with the strata lying obliquely and differentially eroded to produce ridges and furrows running parallel to the strike. The transect ran nearly parallel with these up a gentle slope from the water's edge to a flat platform, bounded on the south by one of the projecting rocky ridges. At its highest point the island is about 30 ft. (9 m.) above the lake surface. In structure and vegetation it closely resembles the other large islands in the Lake and the numerous rocky outcrops which rise from the marshy expanse between the Lake and Derry-cunihy. Arbutus Island, unlike Ronayn's Island, has never been inhabited, and it has probably been little interfered with in the past apart from the possible removal of some poor oak trees by poachers.

The list of species and their frequencies in the various zones of the transect are given in Table VI. This is supplemented by short descriptions of the zones, and by Fig. 9. In these the figures 0-60, 60-80 refer to the distances in feet from the water's edge, measured on the ground along the base line.

(a) *The bare rock zone, with local hollows* (Fig. 9) (0-40 ft., 0-12 m.). The belt stretching 40 ft. (12 m.) from the water's edge presents two ecologically distinct habitats, namely the exposed ridges and the intervening sheltered hollows. At first these are quite distinct, with distinct plant communities, although many of the species are the same.

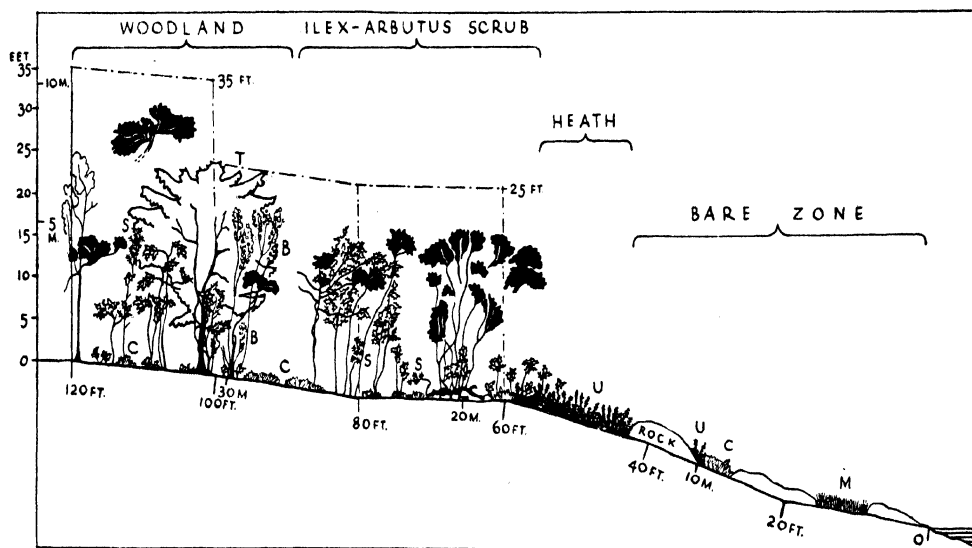


FIG. 9. *Arbutus* island succession; profile diagram through the transect (20 ft. (6.1 m.) wide) showing succession from bare rock to woodland. Symbols as in Figs. 4-7 and, in addition, the large tree (T) is *Taxus*, the black canopy is of *Arbutus*; U, *Ulex europaeus*; M, *Molinia coerulea*. The rocks shown in the bare zone are ridges running obliquely to the plane of the transect and in the diagram this obliquity is emphasized so that the plants of the hollows may be represented.

The *hollows* bear a closed community dominated by *Molinia coerulea* accompanied by quite a rich flora (Table VI) with marsh plants in the lower parts, and plants of drier habitats higher up. These plants are growing on and producing a raw humus up to 40 cm. thick which overlies the hard rock surface. Seedlings of *Hedera helix*, *Sorbus aucuparia*, *Juniperus communis*, *Ilex*, *Ulex europaeus*, *Betula pubescens* and *Taxus* are all found in this zone, but none is more than a few years old.

The ridges separating the hollows are for the most part bare, except for lichens, but in numerous crannies and pockets filled with humus, individual small plants or little communities are established. Seedlings of *Fraginus excelsior*, *Sorbus*, *Taxus* and *Arbutus* are occasional here.

Table VI. *Species list for the transect on Arbutus Island*

Species	Bare rock zone		Heath zone	<i>Arbutus-Ilex</i> scrub	Oakwood
	Hollows	Ridges			
<i>Achillea ptarmica</i>	+
<i>Angelica sylvestris</i>	+
<i>Hypericum pulchrum</i>	+
<i>Leontodon autumnalis</i>	+
<i>Pedicularis palustris</i>	+
<i>Plantago (species)</i>	+
<i>Potentilla erecta</i>	+
<i>Salix atrocinerea</i>	+
<i>Scirpus caespitosus</i>	+
<i>Viola canina</i>	+
<i>Carex panicea</i>	+	+	.	.	.
<i>Carex praecox</i>	+	+	.	.	.
<i>Centaurea nigra</i>	+	+	.	.	.
<i>Myrica gale</i>	+	+	.	.	.
<i>Scabiosa succisa</i>	+	+	.	.	.
<i>Solidago virgaurea</i>	+	+	.	.	.
<i>Hypericum androsaemum</i>	.	+	.	.	.
<i>Hypochaeris radicata</i>	.	+	.	.	.
<i>Sedum anglicum</i>	.	+	.	.	.
<i>Sieglingia decumbens</i>	.	+	.	.	.
<i>Juniperus communis</i>	.	.	+	.	.
<i>Erica cinerea</i>	+	+	+	.	.
<i>Molinia coerulea</i>	+d.	+	+r.	.	.
<i>Ulex europaeus</i>	.	+	4 ft. s.d.-a.	Marginal	.
<i>Calluna vulgaris</i>	+	30 in. a.-l.d.	To 3 ft. s.d.	o.-l.a.	o.-l.a.
<i>Ilex aquifolium</i>	.	+	s. to 12 in.	+	+
<i>Pteridium aquifolium</i>	.	.	o.-l.f.	l.a.	o., puny
<i>Vaccinium myrtillus</i>	.	.	Under	a.	a.-d.
			<i>Calluna</i>		
<i>Sorbus aucuparia</i>	.	Seedlings	0-5 ft.	+	+
<i>Arbutus unedo</i>	.	Seedlings	.	+	2-3 in. etiolated
<i>Hedera helix</i>	.	.	Seedlings	f.	f. and seedlings
					l.a.
<i>Hymenophyllum tunbridgense</i>	.	.	.	l.f.	
<i>Lonicera periclymenum</i>	.	.	.	o.	l.
<i>Rubus fruticosus</i> agg.	.	.	.	r.	r.
<i>Betula pubescens</i>	+
<i>Melampyrum pratense</i>	+
<i>Taxus baccata</i>	+
<i>Quercus sessiliflora</i>	+

(b) *The Ulex-Calluna zone of heath, 40-60 ft. (12-18 m.).* By the accumulation of humus, more rapidly in the hollows than on the ridges, there is ecological convergence. The depth of humus increases with distance from the water's edge; on the ridges it is 4 in. (10 cm.) deep at the margin of continuous *Calluna*, while at the back of the zone it reaches 23 in. (60 cm.). The number of species is reduced and a more uniform heath vegetation is formed in which either *Calluna vulgaris* or *Ulex europaeus* is dominant.

The *Calluna* attains an average height of 30 in. (80 cm.), *Ulex europaeus* 4 ft. (1.2 m.) on the ridges and 6 ft. (1.8 m.) in the hollows, thus obscuring the inequalities of the ground. The hollows are narrower here, and first by shading

from the side, later by colonization of the hollows, *Ulex* kills out *Molinia*. *Erica cinerea* is frequent, while an occasional small plant of *Vaccinium* survives under the shade of *Calluna*. Well-grown *Juniperus communis* also occurs occasionally.

Seedlings of *Ilex* and *Taxus* are present and older plants of *Sorbus* (up to 3 ft. (1 m.) in height) and one of *Ilex* (1 ft. (30 cm.)) are well established.

(c) *The Arbutus-Ilex scrub*, 60–90 ft. (18–27 m.). In the middle of this zone there is a change in the topography; the ridges end abruptly in boulders and give way to a flat and more even surface bounded on the south by a steep rocky outcrop. The zone is dominated by *Arbutus* and *Ilex*. There are few trees of *Arbutus*, but these produce, from their fallen stems, numerous shoots, up to 20 ft. (6 m.) high. Their tops are only slightly wind blasted. The *Ilex* individuals are more numerous, varying in height up to 20 ft. (6 m.) and they are invading as a well-defined though narrow belt the *Calluna-Ulex* heath. That advance has taken place, is clear from the dead *Erica* and *Calluna* under the shade, while just outside the holly belt, *Calluna* reaches 3 ft. (1 m.). Seedlings of *Hedera*, *Ilex*, *Taxus* and *Sorbus* and small plants of the last three are frequent or locally abundant. One seedling *Arbutus* occurred under dense shade. Light-loving species are in process of elimination, while in the shade *Vaccinium* is abundant, and *Lonicera* (o.), *Rubus* (r.) and *Hymenophyllum tunbridgense* (l.a.) appear for the first time.

(d) *The oakwood*, 90–120 ft. (27–37 m.). The centre of the flat portion of the island is occupied by an oakwood rather like type III. It does not appear very clearly in the transect diagram, which was cut short here and includes only one small oak tree and a large *Taxus*. It will be noticed that *Arbutus* appears here only as canopy; the trees producing this grow outside the transect on the exposed continuations of the rocky ridges already mentioned. Thus *Arbutus* does not form a component of the oakwood proper and it only survives here on the higher, more rocky parts by the continued production of adventitious shoots from old trunks. The oakwood itself is far from uniform, but the following description applies to that part included in the transect and its neighbourhood.

The soil on which the wood occurs is largely composed of raw humus, between 35 and 65 cm. deep, over rock. There are few boulders. The trees are *Quercus sessiliflora*, *Betula pubescens*, *Sorbus aucuparia* and an occasional *Taxus*; they average 20 ft. (6.1 m.) in height, and never exceed 25 ft. (7.6 m.). *Quercus* is probably the most abundant, but is not dominant. *Ilex* forms a rather sparse and very irregular under-story and its seedlings and adventitious shoots contribute patches of low straggly growth. The canopy is locally more dense than in type III owing to the shade cast by *Taxus* and marginal *Arbutus*.

The subsidiary vegetation is largely made up of *Vaccinium* up to 18 cm. high, non-flowering, and *Calluna vulgaris*, reaching 80 cm., flowering in the

lighter patches and dying under shade. *Pteridium* is locally frequent, but always puny. *Lonicera* is occasional and *Hedera* frequent; the ivy grows on *Betula* and *Ilex*, and creeps on the ground. *Hymenophyllum tunbridgense* grows well on the exposed roots of *Taxus*, and on rocks. *Melampyrum pratense* flowers freely; *Rubus* is rare.

Seedlings of *Hedera*, and seedlings and small plants of *Ilex*, *Taxus* and *Sorbus* are frequent. In one place two 2-3-year-old seedlings of *Arbutus* occurred under the shade of yew, but they were etiolated, and probably will not survive.

The following species are all rare or local on the island but did not occur in the transect:

Agrostis stolonifera, *Blechnum spicant*, *Hymenophyllum peltatum*, *Dryopteris aemula*, *Polypodium vulgare*, *Potentilla erecta*, *Prunella vulgaris*, *Rhododendron ponticum* (one plant, 3 ft. high), *Spiraea ulmaria*, *Viola sylvatica* agg.

The mosses and hepatics of the transect were listed but not in the detail required for a full account. Thirty species are recorded for the whole transect. In the bare zone, there are largely species not represented in the Derrycunihy types, e.g. *Campylopus atrovirens*, but as one passes towards the wood the others appear and in the wood itself the species and communities resemble those of type III, though most of the "closed boulder assciule" was found on bare ground.

THE ECOLOGICAL STATUS OF *ARBUTUS UNEDO*

Arbutus grows about the Upper Lake on sandstone. Its most common habitats are the rocky margins of streams, the rocky outcrops rising from the *Molinia* marsh (Fig. 3), the steep faces of heath-clad slopes where scattered small trees of *Quercus*, *Betula*, *Sorbus*, *Ilex* and yew also occur, and the *Ulex-Calluna* heath of the slopes of the islands in the Upper Lake. It also occurs in the earlier stages of the physiographic succession leading to type I, along wood margins, and rarely, as in type III, in the wood itself. It is common in similar habitats on the limestone near Muckcross and round the Lower Lake, but here its behaviour was not carefully examined.

Particular attention was paid to the occurrence of seedlings. These are fairly numerous and nearly all are found in pockets of "mor" in rock crannies and depressions, or in open well-lighted places. The pH of one sample of soil from the roots was 3.8. Seedlings are also occasional in mineral soil. They are rarely found under shade. Young plants and bushes are scarce, and most were seen in the island heath. There is no evidence to show that *Arbutus* can grow up under the shade of other plants; it appears to be a light-loving plant in west Ireland.

The occasional existence of *Arbutus* trees in small oakwoods of type III is explained by a peculiarity in its growth. In the rocky places where it becomes established the roots are necessarily shallow and old trees fall over to a leaning

or horizontal position. The persistence of the plant under these conditions is, however, remarkable; the old crown dies, and the old trunk may become partly decayed, but numerous new shoots arise from it and grow erect under partial shade. In this way the crown of the tree may actually be found inside the wood and convey a wrong impression if seen only from a distance. No tree was seen with its crown completely shaded by an oak canopy.

So many of the fragments of oakwoods (e.g. west of Derrycunihy) end abruptly at the rocky outcrops favoured by *Arbutus* that it is difficult to find evidence of what happens to *Arbutus* in the succession on even ground. From what little evidence we have, we believe that *Arbutus* becomes established before the heath covers the ground, or in open areas within the heath. It survives through the phase of heath and becomes incorporated in the *Arbutus-Ilex* scrub. But it seems clear that its presence or absence in the oakwoods is finally determined by the heights reached by the oak and *Arbutus*. In western Ireland *Arbutus* rarely, if ever, grows taller than 35 ft. (10.6 m.), and in woods where oak exceeds this (as in types II and III), *Arbutus* rarely survives; in type III, on the other hand, its crowns occasionally form part of the tree canopy. We have no evidence to decide whether it can reproduce itself in such woods; only the negative evidence may be cited that we saw no small plants.

From the evidence at our disposal we conclude that *Arbutus* on the sandstone at Killarney is a normal constituent of the seral stages leading to oakwood, but it is absent from the climax except where the oak is of poor growth and unable to raise its crown above that of *Arbutus*.

GENERAL DISCUSSION

The chief interest of Derrycunihy wood is physiognomic rather than floristic. The flora is poor and the more exacting herbs and shrubs, which are found in the neighbouring oak-ash woods at Muckross, are doubtless excluded by the high acidity of the soils over sandstone. And in the preclimax stages of type I other species like *Arbutus*, which can grow on alkaline as well as very acid soils, are, as we have seen, eliminated when development to woodland takes place, or they survive only where the oaks are too small to shade them. The flora of Derrycunihy wood is in fact much the same as that of oakwoods on similarly acid soils elsewhere in Great Britain. Twenty-two of the thirty herbaceous species are found in nearly every British vice county; the remaining eight species have an Atlantic distribution. Of these the three common species are ferns, the others are local and, with the exception of *Euphorbia hiberna*, not typical woodland plants.

The poverty in vascular plants is in striking contrast to the wealth of bryophytes; probably over 75% of the whole British bryophytic flora is found in Kerry, and in Derrycunihy wood (including small flushes, etc.) there

are at least ninety species, three times the number found in a mature Cambridgeshire oakwood. But the outstanding feature of the wood is the abundance and vigour of the evergreen *Ilex aquifolium*, *Calluna vulgaris* and *Vaccinium myrtillus* and of the bryophytes and *Hymenophyllum* which carpet the boulders and reach far into the tree crowns. These species are characteristic of the oceanic climate of Western Europe, falling off in number and vigour, or disappearing altogether as the climate changes from oceanic to continental. Even within the limits of the British Isles the change is marked, and nowhere perhaps in them, except at Killarney does *Vaccinium myrtillus* reach a height of 7 ft. (210 cm.) or *Calluna vulgaris* form a heath with an average height of 4 ft. (120 cm.), and individual stems of 220 cm. (Rübel).

From the scanty information in the literature, from data kindly supplied by Mr Hyde and Dr Watson and from our own observations, it is clear that *Ilex* grows better and more abundantly in the west of Britain or near the coasts (e.g. at Woodbridge in the east, in the New Forest in the south). But while *Ilex* is frequent in many oakwoods, whether dominated by *Quercus sessiliflora* or by *Q. robur*, only at Wastdale and at Manaton and Buckfast in Devon have we seen it so abundant as to suggest comparison with the Killarney woods. In many ways the Devon oakwoods closely resemble those of Ireland and a more detailed account of them and of the oakwoods of central and west Wales is to be desired. Praeger (1934) gives brief notes of various scattered relict oakwoods in Ireland, as at Glendalough (Wicklow), Inchiquin, Lough Cann, Lough Gill; in these woods the holly is abundant, though only for Glendalough does he describe a "second layer" in the wood—of *Ilex* and *Corylus*.

In this country the oak-holly woods are centred in the more oceanic west. The ash-oak and oak-hornbeam woods are mainly eastern. Soil variation however plays an important part, so that on suitable soils, even at Killarney, ash-oak woods are found. A similar distribution and relationship between the Querceto-Betuletum ilicetum of Tüxen (1930, 1936: Querceto sessiliflorae-Betuletum, subatlantic variant, 1937) and Quercetum-Carpinetum is found on the Atlantic seaboard of the Continent; the oak-holly woods are essentially Atlantic and outliers eastwards are found only on the higher ground where the climate is wetter. The oak-hornbeam woods, on the other hand, are widespread in central Europe and variants of them on suitable soils occur in western France.

Not only are the Killarney oak-holly woods linked with those of the mainland of Europe, but they are, as Rübel (1912) has shown, floristically related to and physiognomically reminiscent of woods in the western Mediterranean. The extension of *Arbutus unedo* to Ireland is paralleled in western North America by the extension of *Arbutus menziesii* (and *Quercus garryana*) from the broad-sclerophyll forests of California to Vancouver Island (Braun-Blanquet, 1932), where temperate evergreen forest prevails. Evergreen forest is also found in South America and New Zealand in places with a climate

similar to that of west Ireland, and we are of the opinion that the Killarney oak-holly woods represent, with the species available, the nearest approach in the British Isles, if not also in Europe, to evergreen hygrophilous forest.

The absence of evergreen tree dominants at Killarney may be due to the sifting action of past climates and geographical barriers. The tropical or Malayan flora of the Eocene and Oligocene in the south of Britain gave way, towards the close of the Pliocene, to a flora (Cromer beds) which is essentially similar in climatic relationship to that of Norfolk to-day. American conifers now absent from Europe were present in preglacial times in western Europe and it is possible that evergreen forest survived in Ireland down to the Ice Age. If so, then the dominants were destroyed in the glacial periods. The existing forests are dominated by species which have survived, or colonized since then; they are deciduous, but it seems that the climate is permissive to the dominance of evergreens.

SUMMARY

This paper gives an account of the natural oakwoods (*Quercetum sessiliflorae*) of Killarney, south-west Ireland. It provides an accurate description, with profile diagrams drawn to scale, of the three major types of such woodland at Derrycunihy, on the acid soils. These are considered to be important variants of the climax community and their description offers a basis for their comparison with oakwoods elsewhere in Europe.

Some account is also given of the soils of the region and of the bryophytic communities within the woodlands.

An example of plant succession from bare rock to oakwood on *Arbutus* Island is described, and the ecological status of *Arbutus unedo* at Killarney is discussed.

The conclusion is reached that the Killarney oakwoods represent the nearest approach in the British Isles to evergreen hygrophilous forest.

ACKNOWLEDGEMENTS

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We are indebted to Dr Ll. Praeger, Dr Watson and Mr Hyde for notes on woodlands, to Mr R. Seeley of Kew for information on the distribution of *Arbutus*, to Mrs L. Porter of Cork for help with the lichens and to Dr H. Godwin who has read the manuscript. It is a great pleasure to acknowledge the kindness of Mr R. K. A. Kennedy, the agent of the Kenmare estate, who obtained for us permission to work in the woods, took a great deal of trouble in arranging for a camping site and in the building of a hut and at all times placed his knowledge at our disposal.

REFERENCES

- Braun-Blanquet, J.** *Plant sociology*, Eng. ed. New York, 1932.
- Davis, T. A. W. & Richards, P. W.** "The vegetation of Moraballi Creek, British Guiana, Part I." *This JOURN.* **21**, 378, 1933.
- Godwin, H.** "Studies in the ecology of Wicken Fen. III." *This JOURN.* **24**, 101, 1936.
- Martin, N. M.** "Some observations on the epiphytic moss flora of trees in Argyll." *This JOURN.* **26**, 82, 1938.
- Praeger, R. Ll.** *The Botanist in Ireland*. Dublin, 1934.
- Richards, P. W.** "The bryophytic communities of a Killarney oakwood." *Ann. Bryol., Hague*, **11**, 108, 1938.
- Rübel, E. A.** "The Killarney woods." *New Phytol.* **11**, 54-7, 1912.
- Tüxen, R.** "Über einige nordwestdeutsche Waldassoziationen von regionale Verbreitung." *Jb. geogr. Ges. Hannover*, 1930.
- Tüxen, R. & Diemont, W. H.** "Weitere Beiträge zum Klimaxproblem des westeuropäischen Festlandes." *Mitt. Naturw. Ver. Osnabrück*, 1936.
- Tüxen, R.** "Die Pflanzengesellschaften Nordwestdeutschlands." *Mitt. floristisch-soziologischen Arbeitsgemeinschaft Niedersachsen*, **3**, 1937.
- Watt, A. S.** "On the ecology of British Beechwoods. Part II." *This JOURN.* **12**, 182, 1924.
- Watt, A. S.** "Studies in the ecology of Breckland. I." *This JOURN.* **24**, 119, 1936.

PROPOSED NATIONAL ATLAS OF BRITAIN OR THE BRITISH ISLES

At the Cambridge meeting of the British Association (1938) a Committee was appointed under the Chairmanship of Prof. Eva G. R. Taylor (University of London) to consider the possibility and desirability of producing a National Atlas of Great Britain and Northern Ireland, or alternatively of the British Isles. The latter scheme has overwhelming scientific advantages, but presents certain technical difficulties.

The proposed atlas would aim at a strictly objective and scientific presentation of the natural conditions, natural resources and economic utilization of the land (and adjacent sea), of the history and prehistory of the country, and of the distribution, occupations, movement and social conditions of the population. Besides presenting for the first time in collective form and on a uniform cartographic plan the results of the various surveys, returns and censuses made by Government departments, the promoters would desire to utilize much of the information gathered by research workers in particular fields—by geologists, pedologists, meteorologists, biologists, archaeologists, historians, sociologists and geographers.

Representatives of the Council of the British Ecological Society who are also members of the Atlas Committee undertook to bring the project before the Society with the object of securing its approval and support, and the matter was discussed at a recent meeting of Council. General approval was expressed and a small committee was formed to consider possible and desirable contributions to the Atlas which the Society might sponsor. It is desired to bring this matter to the notice of the membership and to invite suggestions and offers of co-operation in the preparation of suitable maps illustrating the distribution of British plants and animals, of vegetation, and of other data of biological interest. The following are some preliminary suggestions.

1. A general map or maps of England and Wales (or Great Britain, or the British Isles) showing such broad features of vegetation and land utilization, including the distribution of live stock, as might prove possible on a relatively small scale.
2. A general map showing the distribution of the larger areas of certain well marked and localized plant communities, e.g. salt marsh, sand dune, shingle beach, fen, bog (or moss), Callunetum.
3. A map or maps of one or more areas in which the vegetation has already been carefully mapped (primary survey) and which show clear correlation between vegetation and physiography and/or soil type. Possible examples are C. E. Moss's map of North Derbyshire, and (if Eire is included in the scheme) Pethybridge and Praeger's map of the district south of Dublin.
4. If sufficient data are available, a map of an area showing broad correlation between vegetation types and the distribution of some group of animals (or maps of comparable plant and animal elements).
5. The central English canal system to demonstrate the direct means of dispersal of freshwater organisms between the main river systems with small illustrative maps of one or two typical species of freshwater plants and mollusca.
6. A general detailed map of the vice-comital and provincial divisions in use for plant and animal censuses.
7. Maps showing distributions of typical contrasted groups of plant and animal species (geographical "elements") within the British Isles.

8. One or more maps showing the rate of spread of particular species for which data are available.

9. Maps illustrating the pre-history and history of vegetation, combined or correlated with archaeological maps.

10. Distributions of some typical marine organisms in coastal waters indicating divisions for census records.

It should be clearly understood that the above are no more than some first suggestions for maps illustrating biological data which members of the B.E.S. Committee think it might be possible and desirable to include. It will also be understood of course that the final decision as to what can be included must rest with the British Association Atlas Committee. Members of the Society are invited to send comments, further suggestions, and/or offers of co-operation to the Hon. Secretary, Dr H. Godwin, Botany School, Cambridge.

REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

VOL. 7, No. 2, NOVEMBER 1938

THIS number contains sixteen papers (dealing with ecology in Great Britain, the Faroes, Canada, Africa and Java), seven reviews, 146 notices of publication on animal ecology, and an obituary notice of the late Prof. A. E. Boycott.

A. C. Hardy and P. S. Milne have an important paper describing their researches on insects and other invertebrates floating high in the air, which they collected by means of aerial tow-nets attached to kites. They show that there is a very large amount of life in these zones (up to 2000 ft.) and that this insect drift must have important ecological and economic significance. These studies concerned mostly animals with weak flight floating in the wind. Katherine Fisher (Mrs K. Grant) gives the results of several years' enquiry into the migratory movements of the silver-Y moth (*Plusia gamma*) which periodically invades this country. In this case the movements (which are partly seasonal) are little influenced by winds.

There are studies of bird ecology from the Arctic, Temperate and Tropical Regions. A. J. Marshall records the occurrence of a pause in activity among some Spitsbergen birds during the "night", although in summer there is continuous daylight. In other species activity in the population was continuous. Three censuses of breeding gannet colonies for Myggenaes Holm, Faroes (by H. G. Vever and F. C. Evans), Ailsa Craig (by H. G. Vever and James Fisher), and Noss, Shetland (by James Fisher and L. S. V. Venables) continue an organized attempt to work out the total breeding population of the gannet species. J. M. Winterbottom describes the results of transects of woodland in Northern Rhodesia, during which the birds seen were counted, while R. E. and W. M. Moreau discuss the significance of territorial habits among two species of bishop-birds (*Euplectes*) in Tanganyika. They show that in one species territorial habits limit density, but not in the other.

Food studies include an analysis of the crops of partridge chicks by J. Ford, H. Chitty and A. D. Middleton, in which the change-over from insect to plant diet during the first month of life is proved. K. R. Allen relates analyses of the food of trout in Windermere to various population movements and the age of the fish. Another fresh-water investigation, by R. Douglas Laurie and J. R. Erichsen Jones, is concerned with the recovery in the fauna of the River Rheidol in Wales, after the abandonment of lead-mining in the area, which had formerly been polluted by lead effluents.

Studies on mammal populations include the second instalment of the Canadian Arctic Wild Life Enquiry for 1936-7, assembled by D. Chitty. In this the recovery of arctic fox populations in the Eastern Canadian Arctic is shown in relation to similar increase of lemmings and snowy owls. F. C. Evans and H. G. Vever describe a biological survey of the Faroe mouse and its distribution on the Faroes.

There are two insect population studies. J. Ford gives a long account of the population counts he made of Collembola and mites living in *Bromus* grassland near Oxford, and supplements the detailed technical record with a general discussion of the philosophy of ecological investigation of communities. W. Pickles continues his studies of the numbers and biomass of ant populations in Yorkshire, and is able to show that *Acanthomyops flavus* forages underground for food and has therefore definite territories. There is also a paper by G. B. Thompson on the numbers of different kinds of ectoparasites found on rats in Java.

Reviews deal with the *Journal of Ecology*, a new glossary of ecological terms, a text-book on ecological animal geography, deer and sea-bird population studies, the history of Richmond Park, and modern phenology.

CHARLES ELTON.

SOILS

Del Villar, E. H. *Los Suelos de la Peninsula Luso-Iberica.* (Soils of the Lusitano-Iberian Peninsula.) Pp. 416, with coloured map, 59 tables and 28 engravings. English text, somewhat abridged, by G. W. ROBINSON. Thomas Murby and Co. 40s. net.

This book appears to be of considerable importance to pedologists and of considerable interest to ecologists. It deals with the soils of an area which shows an extremely wide range of climatic conditions, from high humidity to extreme aridity, and comparable to the range from the south of Ireland to arid North Africa. This range of climates, moreover, operates on a country characterized by a striking diversity of surface and geological structure, and with a history of many centuries of agricultural exploitation. The classification and description of the soil types developed in the Iberian Peninsula is thus of great general value and Prof. Del Villar's interpretation of the primary data is of such general interest that it may well modify existing ideas on soil development and classification.

In this work soils are classified first into *series*, the emphasis being laid on the dynamic implications of this word, which is also preferred because it leaves the word *type* free to be used as a general term without special categorical significance. Then Prof. Del Villar tentatively distinguishes eight *series* of soils as follows:

Aerobic soils:

(a) *Saline series*, with a high proportion of soluble salts.

(b) *Alkaline series*, soluble salts low, but a high proportion of sodium in the absorbing complex.

(c) *Calcareous series*, with calcium carbonate in the edaphic horizons.

(d) *Allitic series*, with humus as a fugitive constituent and a high proportion of sesquioxides resulting from leaching.

(e) *Acid humus series*, with soluble acid humus and marked leaching of sesquioxides from the upper horizon.

(f) *Siallitic series*, with "mild" humus and less intensive leaching.

Soils at times anaerobic:

(g) *Alluvial series*, with disturbances due to intermittent flooding.

(h) *Gley series*, with permanent waterlogging from ground water.

Implicit in this classification is the idea that each soil is associated with a climax vegetation and, accordingly, it is not surprising to find that the *series* may include developmental *stages* which may be either immature or post-mature. The soils on mountain slopes, for example, usually represent immature *stages*. Further, emphasis is laid on the fact that each soil series may include various *phases*. This the *natural phase* is that shown by a soil under the vegetation which has produced it. The same soil under cultivation gradually changes its character, the primary A horizons tend to be modified and mixed by tillage and manuring, and the soil finally assumes the *agropedic phase*. Similarly, one can distinguish a forest phase under woodland which may, on the destruction of the forest give a prairie phase under grassland or some equivalent modification. The whole system is regarded as very fluid and the existence of intermediate or transitional types of soil is freely admitted as a necessary result of a really natural classification. To the ecologist, perhaps, it may seem particularly attractive because of the ecological basis running through it.

This outline of the main argument of the book gives perhaps a better general idea of its contents than a more detailed description might. The author includes, however, a number of criticisms of current views, some of which bear upon the terminology employed. For example, he considers that there are no true podsoles in the north-west of the Peninsula, the leached A2 horizon being absent in that area. He therefore regards podsoles as being characteristic of

high latitudes and, also, does not consider the term podsol as the best comprehensive name for soils whose main characteristic is the possession of unsaturated humus. Such terms as "brown forest soils" (the Braunerde of Ramann) also come in for criticism on the grounds that both forest soils and brown soils of a very different character can be found. In the Peninsula, red soils are also found in this series, though these are non-calcareous and hence cannot be described as "terra rossa". The whole group of soils intermediate between the acid-humus series and the calcareous series is therefore included in the siallitic series. Many of these discussions add to rather than detract from the attractiveness of this classification to the ecologist and another useful feature of the book is that data for vegetation types are given with the primary data. The latter include full tables of chemical analyses along with data for rainfall and altitude. There is an excellent coloured map showing the distribution of the main soil types. Finally, a word of congratulation is due to Prof. Robinson for his admirable summaries of the text.

W. H. P.

Stewart Sharpe, C. F. *What is Soil Erosion?* Pp. 84 and 100 photographic illustrations. U.S. Dept. of Agriculture, Misc. Publ. No. 286.

Problems of soil erosion have been so much in the foreground recently that this publication, consisting of photographs with explanatory letterpress, has appeared at an opportune moment. It gives numerous and striking illustrations of what may happen when the natural vegetation cover is destroyed or when soils are bared by fire or by overgrazing. Under such conditions and especially on sloping surfaces, the rate of erosion exceeds the rate of soil formation and there are resultant changes in the appearance of the soil surface. Various aspects of these problems are considered, the regional differences in erosion and natural land forms, erosion by rainfall and running water, mass movements of soil, aspect effects, and erosion by wind. The illustrations are all North American and they include some of more or less familiar type, such as those of the mobile sand-dunes to the east of Lake Michigan. But there are also many other very striking ones, notably two side by side, though not on the same scale, comparing the Yellowstone River Canyon with a derelict agricultural area in Illinois. Equally striking is a comparison of the interiors of a Virginian woodland in its natural state and a corresponding woodland in which the humus cover has been destroyed by grazing and trampling. In the latter case, the level of the soil has been lowered many inches below that of the origin of the tree roots. Still another photograph of interest shows the steplike structures produced on steep slopes by soil movements.

W. H. P.

AFRICAN VEGETATION

Herbaceous communities within the Central Forest area of the Belgian Congo

Robyns, W. *Contribution à l'étude des formations herbeuses du District Forestier Central du Congo Belge.* Extrait des Mémoires publiés par l'Institut Royal Colonial Belge. T. 5. 1936.

The forests of the Belgian Congo are distinguished as "ombrophile" and "tropophile". The former are the forests proper, and comprise two types: (a) the Central Forest, occupying the whole Congo Basin, and (b) the Mountain Forest, which, under humid climatic conditions, occupies the mountain slopes in the eastern part of the colony, at an altitude of from 1500 to 2400 metres. The "tropophile" type is represented by the "open forests" of the Haut-Katanga and Haut-Kasai; these are in reality tree-savannas of distinctly xerophilous character. Each of the three forest types presents its own complex of ecological problems; in this communication, the author deals only with those of the *Central Forest Area*, enquiring especially into the origin and extent of the "clearings" which break the continuity of the forest.

These clearings are herbaceous formations of varied type, being due to different local causes; they may be classified as follows:

I. *Terrestrial formations*:

- A. Edaphic savannas.
- B. Climatic savannas.
- C. Secondary savannas.

II. *Aquatic formations*.

I A. *Edaphic savannas* are natural formations, determined principally by the nature of the soil and subsoil, which does not, in these areas, permit the occurrence of forest; they are herbaceous clearings, always of small extent, and are of two quite distinct types, namely: those on sandy, or loamy to clayey soil (*terre meuble*), and those on laterite. The first type, known as "Esobes", are localized in the swampy forests in the western and most depressed region of the "central basin", following the channels of the Busira River; in no case do they occur on the plateaux or water-sheds. They have a very uniform flora, of which the dominant constituent is *Hyparrhenia diplandra* (Hack.) Stapf (Gramineae), and are to be found generally very near to the watercourses, from which they are separated only by a strip of "gallery forest", so that they must be considered, in general (as for example at Coquilhatville), as riverine formations, occupying old sandbanks formed by change of river-bed, or old, dried-out lagoons. These *Hyparrhenia* savannas tend to regress and disappear owing to the gradual invasion of the forest, so that they mark a stage in forest-evolution.

The savannas on laterite are situated in the Ubangi area, and at the edge of the forest; their flora is very uniform and very limited in species, the dominant being *Ctenium Newtonii* Hack. (Gramineae). The origin and evolution of these savannas is not known.

I B. *Climatic savannas* occur in the northern and southern fringes of the forest; they are limited to the western part of the "central basin", and are more numerous in the south than in the north. They have a vegetation and a flora much more varied than those of the edaphic savannas, and on the whole similar to those of savannas situated outside the forest area; certain of them show forest-evolution stages.

The floristic relations between the Esobes and the climatic savannas suggest a genetical connexion of the two types: climatic savannas would appear to have evolved from edaphic savannas of the Esobe type.

I C. *Secondary savannas*, the result of the action of biotic factors, are of two kinds: "anthropic" savannas, produced by human agency, and elephant clearings.

Anthropic savannas occur in all the Central Forest area, round European settlements and native villages, and are generally small in extent. They are essentially unstable formations, composed of ruderal species, and gradually and naturally revert to forest when abandoned.

Elephant clearings are of only very small extent.

II. *Aquatic formations* occur on the low banks of watercourses, and on islands, as bands of varying width. They are of two types: "agrostologic" or Gramineaceous formations, and Cyperaceous formations.

The *Gramineaceous formations* are localized, for the most part, in the same areas as the "Esobe" savannas; they represent the initial stage of the colonization of submerged land, contributing to its elevation. Through the succeeding stages of "suffruticetum", "fruticetum" and "gallery forest", is reached the climax of the region, the "swampy forest". Certain of these grass formations may evolve into Esobe, and thus, they constitute the initial infra-aquatic stage of an edaphic savanna; this is the case for the swampy riverine meadows of *Jardinea congoensis* Franch. established in lagoons, which, by the accumulation of alluvium, may be transformed gradually into swampy or damp *Hyparrhenia diplandra* Esobe, the progressive series of vegetation being *Jardineetum congoensis* → *Hyparrhenietum diplandrae* → fruticetum → swampy forest (climax). It is not impossible that, under certain conditions, the *Jardineetum congoensis* may evolve directly into fruticetum.

The *Cyperaceous formations* are much more rare than the grass formations, and they are scattered through the whole Central Forest area. Their evolution is not known, but it has probably followed, broadly, the lines of evolution of the grass formations. H. B.

FOREST ECOLOGY

Romell, L. G. (i) Markreaktionen efter gallringar och dess orsaker. *Norr. Skogs. Tidskr.* 43, 1, 1938. (With English summary.) (ii) A trenching experiment in spruce forest and its bearings on problems of mycotrophy. *Svensk Bot. Tidskr.* 32, 89, 1938.

These two papers bear upon different aspects of the same problem and, indeed, of the same experiments. In the first, the author points out that foresters no longer explain the effect of thinning a woodland as due merely to the effect of increased light upon tree growth. They accept the ideas that there must be not only a decrease of root competition but also a change in the general soil reaction, just as there is after felling. It is still the case, however, that the soil effects are usually ascribed to the alterations in humidity and irradiation caused by increased exposure and resulting from the more open canopy. The author points out, however, that all the effects of thinning known cannot be explained on this assumption and, further, that there are a number of experiments on record in which trenching (without touching the stand) has produced effects of a similar type which also require explanation. It is suggested that the real basis of the thinning effect is a soil fertilization due to the killing off of the tree mycorrhizas and consequently to greater availability of nitrogen.

The second paper describes recent trenching experiments by the author bearing upon this question. In a poorly growing spruce forest with a *Vaccinium* ground flora, certain areas, varying between 6 and 52 square metres, were isolated by trenches and by foot-deep iron sheeting sunk into the trenches before the latter were filled up. Tree roots were naturally cut through in sinking the trenches. The isolated areas contained no mature trees though occasional seedlings were present. They enclosed about 12% of the area treated and about 600 square metres in all. An adjacent plot was given at frequent intervals a heavy fertilization with ammonium nitrate solution. At the end of the following growing season striking responses were shown both by the isolated and by the fertilized areas. In both cases, the ground vegetation was a much darker green and so were the tree seedlings present in the treated areas. Further, there was a marked lag in the autumnal colour-changes on these areas. These symptoms are regarded as evidence that isolation by trenching causes a great increase in the availability of nitrogen. In the author's opinion this increase is too great to be due merely to the cessation of competition from trees, it is considered to be due to a green manuring effect caused by the killing off of roots and of mycorrhizas and associated fungi as well as to the stoppage of competition from these organisms. The mycorrhizal fungi are supposed to be unable to break down organic residues in the humus and thus need to be in contact with an appropriate host plant to obtain their carbohydrate foods. Thus inside the trenched areas all the Hymenomycetes observed to fruit seemed to be saprophytes. On the other hand, just outside the trenches, where much damage to roots and to mycorrhizas must have taken place, a number of species which appear to be obligate mycorrhizal forms fruit with exceptional freedom. It is suggested that the fertilization due to trenching may be equally great here, but that its products are assimilated by the abundant mycorrhizal filaments, many of which must still be in contact with the living trees, their hosts, and so able to obtain the energy foods they require.

W. H. P.

REGIONAL SURVEY

The Cambridge Region. Edited by **H. C. Darby**. Pp. xiii + 234, 58 figures. Cambridge University Press. 6s. net.

This book was prepared as a handbook for the Cambridge Meeting of the British Association (1938), and it was presented to members attending the meeting by the Syndics of the University Press. It is now re-issued in more permanent binding. To many readers of this *Journal* it will already be familiar, and on this account it may be reviewed somewhat more briefly than its intrinsic interest might warrant. By way of general description, one may say that thirty-four contributors discuss in these pages various aspects of the geology, physiography, soils and climate of the district, its biology and archaeology, history and industrial features. Included in these detailed accounts are two botanical contributions by Drs H. Godwin and A. S. Watt. While, because of the number of subjects discussed, the individual accounts are somewhat concise, the treatment as a whole forms an extremely valuable regional survey of the Cambridge district.

Its value lies particularly in the fact that by a combination of circumstances the Cambridge district is representative of much of southern England in its variety of soils and solid geology, and, at the same time, is endowed with two areas, in the Fens and the Breckland, which are of especial and almost unique interest. Further, the district lies athwart what have evidently been main lines of human invasion from the east and, no doubt because of the many active investigators connected with the University, the prehistorical and archaeological description of the area is becoming unusually complete. For these reasons, both the existing vegetation and the history of human activities can be seen in something approaching a true perspective.

Those interested in regional survey in other districts will find the archaeological background especially interesting because the principles are stated and are clearly capable of being applied elsewhere. For example, the evidence is convincing that the clearing of the heavy clay soils was delayed until the Anglo-Saxon settlement. The summary of recent work on the post-glacial changes in the Fenlands is of equal utility and interest. W. H. P.

BIBLIOGRAPHY

Forest Bibliography to 31 December 1933. Compiled and published by the Department of Forestry, University of Oxford. Pp. 201-274. 12s. 6d.

This is the third part of the Oxford Forest Bibliography to which attention was drawn in this *Journal* last year. This part deals with various aspects of forest protection in the widest sense. Section one deals with damages caused by man and the second section with protection against animals and game preservation. Sections three and four deal with atmospheric influences and fire respectively and with control and protective measures against these effects. Weeds, parasites and climbers fall into section five, while all other agencies come in the sixth section, which includes floods, swamps, avalanches and land movements and reclamation works such as drainage and stabilization, shelter belts and the like. The last section is a brief one dealing with fencing.

Carpenter, J. R. *An Ecological Glossary.* Pp. ix + 306, with 6 maps. Kegan Paul. Price 15s.

This work, noticed in the last number of this *Journal* (p. 500), is now published in Great Britain.

PROFESSOR CARL SCHRÖTER

WE deeply regret to receive the news of the death of the oldest Honorary Life Member of the Ecological Society, Professor Schröter, of Zurich, in his 84th year. As his children say in their announcement, his life was long and happy. Certainly no one could have deserved happiness more. His active kindness and helpfulness to colleagues of every nationality and, indeed, to all with whom he came in contact, endeared him to everyone who knew him. There can have been no botanist who was more universally loved and venerated, and his death leaves a gap that cannot easily be filled.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON

5—6 JANUARY 1939

Soirée in the Department of Botany

ON the evening of Friday, 5 January, about 80 members and guests were entertained at a soirée in the Department of Botany, University College, London.

An interesting series of exhibits was shown. Dr F. W. Jane showed a large number of very beautiful drawings and microscopic preparations of a large number of little known British flagellates. Many species of flagellates appear to be rare because not looked for at all, or at the wrong time of the year. Included in the exhibit were many hitherto undescribed species and even genera. A rough classification of habitats was suggested, and the habitat was shown for each of the species. Other exhibits showed the appearance of "annual rings" in sections of the fossil *Lyginopteris*, and vivipary in the fruiting heads of *Dipsacus vulgaris*.

Prof. Salisbury exhibited a series of full-scale drawings of the root systems of dune plants excavated by blowing away of sand. They included *Calluna vulgaris*, *Lotus corniculatus* (80 cm.), *Euphorbia portlandica*, *E. paralias* (130 cm.), *Hypochaeris radicata* (60 cm.) and *H. glabra* (60 cm.), *Ononis arvensis* (150 cm.), *Galium verum* (150 cm.), *Diplotaxis tenuifolia* (70 cm.), *Salvia verbenaca* and *Eryngium maritimum* (155 cm.).

At 9 p.m., Sir Arthur Hill gave an interesting talk on "The Art of living upside-down". He described the reaction of flowers to suspension in inverted positions, and illustrated the resultant types of movement by a large series of specimens, photographs and drawings. He pointed out also the interest of the natural inversion of leaves of *Alstroemeria* and *Bomarea*, and of the positions taken up by the pitchers of *Nepenthes*.

The Annual Meeting

The twenty-fifth annual meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Friday, 6 January, at 10 a.m., the President, Prof. A. G. Tansley, occupying the chair.

Prof. Tansley explained how pressure of work had made him unable to prepare a presidential address, and how the Council had made arrangements for it to be read at a meeting at Easter.

The minutes of the previous meeting were read and confirmed. The resignation of Mrs Hands was accepted and Mr Elflyn Hughes was elected to the membership of the Society. The report of the Hon. Secretary was then read and adopted.

Hon. Secretary's Report for the year 1938

The twenty-fourth annual meeting of the Society was held in the Botany School, Cambridge, on 6 January. On the evening of Friday, 5 January, between 80 and 100 members and guests were entertained at a soirée in the department where a large series of exhibits had been set out.

The Annual Meeting was held on the 6th, and after the business meeting seven very interesting papers were read to the Society. On the following morning a party of 30 under the leadership of Dr Godwin and Mr Tidmarsh, made an excursion by bus through the south-eastern fens and the Breckland margin. The sincere thanks of the Society are due to Prof. Brooks for having given us the generous hospitality of his department.

A new departure in the arrangements of the Society was the holding of an additional

meeting on 20 April in the Botany Department of Bedford College, London, to discuss problems of soil toxicity in Dorset heathland. After introductory accounts by Prof. Neilson-Jones and Dr Rayner, a long and interesting discussion followed, in which several distinguished guests spoke of the problems in relation to their own fields of forestry and soil science. After lunch there followed the inspection of a long series of exhibits illustrating different aspects of the problem. We are greatly indebted to Prof. and Mrs Neilson Jones and their assistants for an extremely profitable meeting.

The Summer Meeting of the Society was held in the University College of Wales, Aberystwyth, from 16 to 21 July. Several expeditions of very great interest were made to Tregaron Bog, to the Dovey dunes and salt marshes, to the Welsh Plant Breeding Station and to the field experiments in the Welsh mountains. A soirée was held on the evening of 16 July and evening meetings were held on the 19th and 20th. About 30 members attended the meeting and a number of these remained after the 21st and were conducted on further local ecological excursions. The Society has seldom had so successful a Summer Meeting and must be extremely grateful to Profs. Newton, Laurie and Stapledon, and their staffs for contributing so wholeheartedly and successfully to it.

In the past year two numbers of volume seven of the *Journal of Animal Ecology* have been published, appearing respectively in May and November; they contain respectively 198 and 226 pages. Twenty-eight original papers were published with 14 plates, in addition to notices and reviews. Notices of publications on Animal Ecology in this volume totalled 288.

Since the last annual meeting there have been issued two numbers of the *Journal of Ecology*, appearing in February and August, and containing respectively 254 and 247 pages with 7 plates. In this volume have been published 26 original papers, as well as notes and book reviews.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill, and accounts of them occur in the current issue of the *Journal of Ecology*.

Since the last annual meeting the membership of the Society has risen from 350 to 363 members. 12 members have resigned or have died, and 25 new members have been elected. Of the present membership list 193 members received the *Journal of Ecology* alone, 116 the *Journal of Animal Ecology* alone, 52 received both *Journals* and one neither.

During the year the Society has suffered the loss by death of several valuable members, among them Mr B. D. Burt and Mr C. F. M. Swynnerton, killed during air reconnaissance in East Africa, Prof. A. E. Boycott, F.R.S., and Prof. J. W. Bews, both men of the highest rank in our science. Prof. Boycott had been president of the Society in 1932 and 1933.

We are glad to note in the New Year's Honour's List the name of Sir R. G. Stapledon, an ecologist in practice and agriculturist in profession.

This year marks the end of the very long and devoted service of Mr Boyd Watt as Hon. Treasurer to the Society. We offer him our deep thanks for his able handling of our affairs and give him our sincerest good wishes.

The Hon. Treasurer made a provisional statement on the financial position of the Society, reporting a considerable positive balance on the year's working (see statement on p. 249). It was proposed from the chair and accepted *nem. con.* that Messrs William Norman and Son be reappointed auditors of the Society for 1939. Similar approval was given for grants of £5 to the Society's transplant experiments and of £10 to the Freshwater Biological Association.

The President then explained to the meeting that in view of Mr Boyd Watt's twenty-five years devoted service to the Society, the Council had nominated him on retirement from his post as Hon. Treasurer for Hon. Life Membership of the Society. This was carried with acclamation.

The alterations of rules proposed by the Council, to give effect to their wish that there should be two Hon. Treasurers and two Hon. Secretaries, were explained by the President and Hon. Secretary and were agreed *nem. con.* (for rules so approved see p. 251).

The meeting then proceeded to the election of officers and council members as follows:

Vice-President: Mr C. DIVER (Dr TURRILL retiring).

Hon. Treasurers: Dr A. S. WATT and Mr V. S. SUMMERHAYES.

Hon. Secretaries: Dr H. GODWIN and Dr G. C. VARLEY.

Ordinary Council Member: Dr O. W. RICHARDS (Dr ASHBY retiring).

The President then mentioned the arrangements for the Easter Meeting, which by the kindness of Prof. William Brown would be held in Imperial College, South Kensington. He mentioned the possible alternatives of the New Forest or Plymouth for the Summer Meeting, and outlined a scheme for a National Atlas, in the preparation of which the Society had been asked to co-operate. The Hon. Secretary briefly indicated the steps which the Council had taken to co-operate with the Forestry Commission in initiating a scheme for Ecological reserves in different parts of the country.

Mr Richard Freeman, Magdalen College, Oxford, was elected a member of the Society.

The President read a letter from Mr Dudley Stamp suggesting the possibility of having a mechanism for life membership of the Society instead of the payment of annual subscriptions: it was agreed to refer the matter to the Council.

At 11.10 a.m., the President opened the symposium on the Reciprocal Relationship of Ecology and Taxonomy. An account of the proceedings will be found in the *Journal of Ecology*. Those who spoke were:

The President	Dr J. Burt Davy	Mr R. Ross
Prof. E. J. Salisbury	Mr A. J. Wilmott	Mr H. Baker
Dr O. W. Richards	Dr B. P. Uvarov	Dr H. Godwin
Dr J. Huxley, F.R.S.	Dr A. R. Clapham	Dr A. S. Watt
Dr D. H. Valentine	Mr C. B. Williams	Mr F. T. K. Pentelow
Capt. C. Diver	Mr C. S. Elton	Dr W. B. Turrill
Mr V. S. Summerhayes		

The discussion continued through the afternoon. In adjourning the meeting the President gave very hearty thanks to Profs. Salisbury and Hill for their hospitality, and to Prof. Salisbury and Dr Barbara Russell-Wells for the trouble they had taken in organizing the soirée and the meeting. The meeting closed at 4 p.m. with tea generously provided by Prof. Salisbury.

EASTER MEETING, 1938

A SPECIAL meeting of the Society was held in the Botany Department, Bedford College, London, at 11 a.m., on 20 April 1938, the President, Prof. A. G. Tansley, in the chair. Several distinguished guests were present by invitation, Dr Crowther, Dr Jacks, Dr Lewis, Dr Guillebaud and Sir Albert Howard.

An informal account was given by Prof. Neilson Jones of some of the characteristics, including that of apparent toxicity, associated with the soils of Wareham Heath. He described the poor growth of conifers in this soil and showed that *Nicotiana* seedlings grown in pots of it only thrive at the margins. He showed that steaming the soil mitigated the effect, and that the vapour from steamed soils produced epinastic movements in tomato like those produced by ethylene. In a film of nutrient agar poured over the soil, fungal spores germinate but the hyphae do not grow: steaming and other pre-treatments remove this effect. The condition of "fused needle" in *Pinus contorta* and *P. insignis* was described and it was said that no pathogen had been detected.

This was followed by a general description, given by Dr M. C. Rayner, of research work done at Wareham since 1932, with special reference to forestry experiments. She showed that seedlings on the sterile soil had no tertiary roots and no mycorrhiza, and demonstrated that good growth and good mycelium go together. The beneficial effects of the addition of composts of straw, hops, sawdust and *Molinia* to the soils were described, and illustrated by very striking photographs.

An extremely interesting and controversial discussion followed, in which many members and guests took part.

After lunch the meeting examined a long series of exhibits dealing with the same problems, and discussed the exhibits with the individual research workers who had produced them.

The discussion was resumed at 3.30 p.m., and some time later closed with a very delightful tea party given in the College. Prof. Tansley expressed the grateful thanks of the Society for the generous hospitality given us by Prof. and Mrs Neilson Jones, their research workers, and the College authorities.

SUMMER MEETING AT ABERYSTWYTH

16—21 JULY 1938

At the kind invitation of Profs. Newton, Laurie and Stapledon, the Summer Meeting of the Society was held at Aberystwyth. The meeting opened with a soirée held in the University College of Wales, at 8.15 p.m. A large number of interesting exhibits had been set out, and during the evening songs were given by some of the University students.

Sunday, 17 July. A visit was paid to Tregaron Bog under the leadership of Dr Godwin. The large west bog is a typical atlantic raised-bog (Hochmoor) with a well developed rand beside the river Teifi, and remains of a lagg where the bog meets the hillside. The highest part of the bog is occupied by very characteristic regeneration complex in which pools and *Sphagnum* hummocks alternate.

Monday, 18 July. The meeting visited the gardens of the Welsh Plant Breeding Station, where Dr Jenkin demonstrated the basis of production of seed for pasturing. He emphasized the need for selection for permanence, leafiness and vigour. He stressed the extremely heterozygous nature of the material and its great phenotypic variation. In the greenhouse Dr Jenkin described the genetical work on *Lolium* and demonstrated the practical methods of performing crosses. He then showed the party the results of some extremely interesting interspecific and intergeneric crosses, drawing especial attention to the doubtful origin of *Festuca loliacea*. This is supposed to be a cross between *F. pratense* and *Lolium perenne* but indistinguishable plants can be produced in other ways. The party went on to the experiments in the Penglais fields, in which were growing rows of clones of many selected and commercial strains of Timothy and other grasses. The close leafy habit of types selected from old pastures contrasted strongly with the stemmy open growth of the commercial strains. The testing for late flowering and resistance to rust were also demonstrated.

Following an improvement in the weather the party travelled in the afternoon to visit the Cahn Hill Improvement Scheme. All the hill-pasture experiments were concerned more or less with the influence of the biotic factor on sward development. Many remarkable effects were shown of treatment by phosphates or basic slag, with or without the introduction of new species such as wild white clover and Yorkshire fog. There was a very marked effect of the transport of minerals with "stock nitrogen" from the lower manured slopes to higher pastures. In particular the effects of night camping by cattle in sheltered hollows at high altitudes, was very strongly marked, such areas showing a great increase in *Agrostis* and establishment of clover.

In the evening at 8 p.m., there was a small exhibit staged in the Botany Department of University College, of various aspects of the work of the Plant Breeding Station, and different members of the staff gave short talks on genetical and ecological aspects of their

work. Dr Jenkin gave an account of genetics in relation to ecology, drawing examples from his very wide experience of the grasses. A point of particular interest was the occurrence of two types of *Arrhenatherum elatius*. The extreme bulbous type is found in arable land, and most hedgerow or wayside plants are intermediate in type. Completely non-bulbous plants have to remain winter green. The *F1* crosses between the extreme types are intermediate. Mr R. D. Williams described his work on genotypes of red clover. The plants are diploid (2×7) and normally cross-fertilized with very common self-sterility. He showed specimens illustrating the determinance of several features such as pubescence, dwarfness, sterility and chlorophyll-deficiency. Marked linkage groups have been demonstrated. Mr W. Davies gave a short description of the grasslands of Wales, and stressed the fact that altitude and geology are not the only factors determining grassland type. He suggested that the dominance of *Agrostis* is largely due to grazing. Prof. Stapledon concluded the series by some general remarks on the ecology of Welsh pastures, again pointing out the great importance of grazing treatment.

Tuesday, 19 July. The party visited Llety-evan-hen to see the experiments of the Welsh Plant Breeding Station on controlled grazing and manuring upon native *Molinia* and *Fescue-Agrostis* swards. The cages under different manurial treatment and strictly controlled grazing showed extremely marked differences from one another, although only begun in 1930. It was very marked that new species made their appearance wherever suitable conditions were created, although no seeds were sown, and although samples showed no buried viable seeds. Within two years the controlled grazing and manuring changed the former *Molinia-Nardus* sward to *Fescue-Agrostis*. After lunch at the Plant Breeding Station the party was shown experiments on grazing and manuring in a valley marsh, where changes as striking as those on the upland pastures were evident. Across one set of plots there was an extremely marked low-fertility strip on the site of a former hedgerow.

At 8 p.m. in the Department, the following series of short papers were given:

"Distribution of hill bogs in Cardiganshire": J. B. JONES.

"Soil Fauna of the Dovey Estuary": Dr WATKIN.

"Preliminary account of Blaen Brefi bog (1300 ft.):": E. G. DAVIES.

"Observations on *Rhynchospora alba*": E. M. CANTON.

"Tregaron Bog": H. GODWIN.

Wednesday, 20 July. The party visited the sand dunes at Ynyslas under the leadership of Mr E. H. Chater. The dunes showed very marked effects of wind erosion and rearrangement, and extensive dune lows and sandy marshes. The effect of blowing sand in promoting the flowering of *Psamma* was very well seen. After lunch the party visited the salt marshes on the shores of the Dovey Estuary, and were shown the evolution of different types of pans from channels and depressions to their final disappearance into close sward. It was quite clear that several different levels of marsh were represented, and distinct phases of erosion and deposition following changes in the course of the Dovey currents.

In the evening there was an exhibition in the Department of Zoology of work on Animal Ecology and the following papers were read:

"Faunistic history of River Rheidol in relation to lead pollution": Dr K. E. CARPENTER.

"Remarks on effect of pollution on plants": Prof. NEWTON.

"The effect of calcium on the toxicity of heavy metal salts to fish": Dr J. R. E. JONES.

At the conclusion of the meeting Prof. Tansley expressed our deep gratitude to our hosts for providing such an exceptionally interesting and satisfactory meeting. He expressed particular thanks to Profs. Newton, Laurie, and Stapledon and the stewards, Mr J. B. Jones and Mr E. G. Davies who had so successfully organized the excursions.

Several members prolonged their stay beyond the official end of the meeting, and were taken on further ecological excursions into the woodland and mountain pastures of the district.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1938

Income

	£	s.	d.	£	s.	d.
Subscriptions received, including arrears, and <i>less</i>						
Payments in advance	475	18	0
Interest on Investments	39	15	0
Interest on Deposit Account	1	5	0
Index volume to <i>Journal of Ecology</i> , vols. I-XX:				41	0	0
Sales	15	18	0
Expenses	3	7	4
				12	10	8

Journal of Ecology, 1938:

Sales: Current vol. xxvi, 1938	£529	8	8
Back volumes and parts	559	0	0
Reprints of papers	41	6	8
Grant: Received per Editor	67	2	0
				10	0	0

Balance (see above, under Expenditure)

	£529	8	8
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Journal of Animal Ecology, 1938:

Sales: Current vol. vii, 1938	£722	19	10
Back volumes and parts	250	18	8
Reprints of papers	95	5	2
				54	17	0

Grant: From Bureau of Animal Population, Oxford ...

Balance (see above, under Expenditure)

	£529	8	8
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Expenditure

<i>Working Expenses:</i>				£	s.	d.
Printing, Stationery, etc.	5	5	6
Postages and Travelling	13	13	5
Bank Charges	1	3	3
Clerical assistance	15	0	0
Meetings, Soirée, etc.	2	4	0
Audit	3	3	0
				40	9	2
<i>Grants:</i>						
Fresh Water Biological Association	10	0	0
Transplants Experiments Fund	5	0	0
<i>Journal of Ecology</i> , Cost <i>less</i> Sales	15	0	0
<i>Journal of Animal Ecology</i> , Cost <i>less</i> Sales	45	11	2
				236	0	10
Balance: Surplus for the Year, carried forward	337	1	2
				192	7	6
				£529	8	8

Journal of Ecology, 1938:

Cost: Paper, Blocks, Printing and Binding	599	4	7
Publishers and Commission	84	9	8
Carriage and Postages	35	5	7
Insurances	4	0	0

Journal of Animal Ecology, 1938:

Cost: Paper, Blocks, Printing and Binding	£722	19	10
Publishers Commission	550	19	10
Carriage and Postages	51	2	5
Insurance	20	13	11
Sundries	6	16	3
Bureau of Animal Population, Oxford, for special services	2	9	3
				10	0	0

	£529	8	8
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BALANCE SHEET AT 31 DECEMBER 1938

Liabilities

Subscriptions prepaid for 1939/31	£	s.	d.
Library Fund
General Revenue Account, Surplus in hand:
Balance at 31 December 1937	...	1087	11 3
Surplus for the Year 1938	...	192	7 6
		<u>1279</u>	<u>18 9</u>
		<u>£1299</u>	<u>12 9</u>

Assets

Cash in Hand at Westminster Bank:	£	s.	d.
Current Account
On Deposit
		<u>27</u>	<u>11 11</u>
Investments at Cost:			
Brought forward, 31 December 1937	...	915	13 0
Bought February 1938, £150 of 3½% War Loan	...	156	7 10
		<u>1072</u>	<u>0 10</u>
		<u>£1299</u>	<u>12 9</u>

Totals held, 31 December 1938:

£850 of 3½% War Loan at cost	£	s.	d.
£200 of 5% Conversion Loan	...	873	10 10
	...	198	10 0
		<u>£1072</u>	<u>0 10</u>

NOTE A. The market value of the above Investments at 31 December 1938:

3½% War Loan at 98	£833
5% Conversion Loan 109½	£219
	<u>£1052</u>

Audited and found correct and as shown by the Account Books of the Society.
The Bank Balances have been verified by Bank Certificates, and also the Investments.

120, BISHOPSGATE, LONDON, E.C. 2.
(Signed) WM NORMAN & SONS,
Chartered Accountants.

1 February 1939.

NOTE B. A further Asset not valued above is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) HUGH BOYD WATT,
Hon. Treasurer.

THE BRITISH ECOLOGICAL SOCIETY

FOUNDED 1913

CONSTITUTION AND RULES

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Hon. Members and Associates as defined in these rules.

3. Applicants for Membership of the Society shall be proposed by one Member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one or more other Members. Such applications shall be made on a form to be supplied by the Hon. Secretaries, and duly filled up and signed by the applicant.

Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

The Secretaries may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if they receive no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on January 1st each year. The minimum Annual Subscription for Ordinary Membership shall be twenty-five shillings (25s.) and for Associate Membership seven shillings and sixpence (7s. 6d.). Members who pay a yearly subscription of 25s. shall have the right to receive post free **either** *The Journal of Ecology* **or** *The Journal of Animal Ecology*. An Annual Subscription of 45s. shall entitle Members to receive post free **both** of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

- (a) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.
- (b) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.
- (c) To vote in the election of Council and of Officers.
- (d) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate Members shall have the right to attend Meetings and Excursions, to obtain through the Secretaries such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of Ordinary Members indicated in 5 (c) and 5 (d).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society not less than twenty-five shillings (25s.) per annum and shall thereby be entitled to receive a copy of **either** of the two Journals of the Society, or on payment of forty-five shillings (45s.) per annum, to receive **both** Journals of the Society. In either case they shall also be entitled (a) to such advice or assistance as the Society can afford, and (b) to send two delegates to the Society's Meetings, to have the same privileges as Associate Members as regards such Meetings.

8. The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the two Hon. Secretaries and the two Hon. Treasurers, with ordinary members of Council.

Officers and ordinary members of Council shall be elected at the Annual Meeting of the Society.

9. Each ordinary member of Council shall be elected for a period of four years, at the end of which time he shall retire. He shall not be eligible for re-election until the Annual Meeting of the year following that of his retirement.

An ordinary member of Council when elected an Officer of the Society shall cease to be an ordinary Council member: on expiry of office the retiring President, Hon. Secretaries, Hon. Treasurers and Hon. Editors shall be eligible for immediate re-election as ordinary members of Council, and the retiring Vice-President shall complete his term of four years' service on the Council.

10. The President and the two Vice-Presidents shall be nominated from among the members of Council. The two Hon. Editors and the two Hon. Secretaries shall retire at the end of each year but shall be eligible for immediate re-election.

11. The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

12. One Vice-President shall be appointed each year and shall hold office for two years.

13. The two Hon. Treasurers shall hold office for three years and shall be eligible for re-election. The Hon. Treasurers shall keep the Society's funds and shall be responsible for collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys and they shall present a financial statement at the Annual Meeting. The financial status and policy of the Society shall be considered each year at a meeting of the Council held as soon as practicable after the audit. The audited accounts shall be published in the Journals of the Society.

14. If any Council member does not attend at least one meeting of the Council during the year he shall retire at the end of the year, but shall be eligible for re-election.

15. At least one fortnight before the Annual Meeting the Secretaries shall circulate to all Members of the Society a list of the members of Council including Officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.

16. Members may propose for ballot at the Annual Meeting the name or names of any duly qualified Member or Members in place of any or all of the Council's nominees.

17. The Council shall have power to co-opt any ordinary Member of the Society to fill vacancies occurring during the year among Council or Officers, the tenure of such co-opted Members to terminate at the next Annual Meeting.

18. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected Honorary Members of the Society.

Such Hon. Members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary Members of the Society.

19. The Annual Meeting shall be held in December or in the following January. At least one other Meeting shall be held later in the year. Further Meetings and Excursions may be held at such times and places as the Council may from time to time determine.

20. At the Annual Meeting the Members of the Society present shall ballot for Officers and Council and consider any other business brought before them by the Council or by any Member, of which four weeks' notice in writing has been given to the Secretaries.

21. Alterations of the Rules shall only be made at the Annual Meeting and require six weeks' notice in writing to the Secretaries and a majority of two-thirds of the Members voting.

22. Members desiring to present communications at any Meeting must give due notice to the Secretaries, stating the nature of the communication and the time required.

23. At any Meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the Rules, not included in the programme.

24. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.

25. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.

26. The subscription price of each Journal to others than Members of the Society shall be as determined by the Council.

27. No Member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

(This revised formulation of the constitution and rules was accepted at the Annual Meeting of the Society, 6 January 1939.)

LIST OF MEMBERS (16 JANUARY 1939)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

- E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
- E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
- A. **Alexander**, W. B., M.A.; University Museum, Oxford.
- A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
- A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
- E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
- E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
- E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
- E. **Andersonian Naturalists' Society** (cf. Glasgow).
- E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
- E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
- E. **Ashby**, Prof. Eric, B.Sc.; The University, Sydney, N.S.W.
- E. **Bacon**, Mrs Alice; The Technical College, Brighton.
- E. **Baker**, H.; University Dept. of Botany, High St., Oxford.
- A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
- E. **Barnes**, Dr B.; 28, Torrington Road, London, S.E. 6.
- A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
- E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
- E. A. **Beauchamp**, R. S. A., B.A.; Connellmore, Cheltenham, Glos.
- E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
- A. **Bertram**, G. C. L., M.A.; St John's College, Cambridge.
- E. **Bhâradvâja**, Prof. Y.; Dept. of Botany, Hindu University, Benares, India.
- E. **Bharucha**, Dr F. R.; 6, Alexandra Road, New Gamdevi, Bombay 7.
- E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
- E. **Blackman**, G. E.; Wick Cottage, Westleigh Av., Putney Hill, London, S.W. 15.
- E. **Bloomer**, H. H.; Longdown, Sunnysdale Road, Swanage, Dorset.
- E. **Bor**, N. L., M.A., D.Sc.; Forest Research Institute, New Forest P.O., Dehra Dun, U.P. India.
- E. **Børgesen**, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
- A. **Bosanquet**, S. J. A.; Fisheries' Laboratory, Lowestoft, Suffolk.
- A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
- E. **Boyd**, L.; Royal Botanic Gardens, Edinburgh.
- E. **Bracher**, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
- E. **Braid**, Major K. W.; 6, Blythswood Square, Glasgow.
- E. **Braun**, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
- E. **Brenchley**, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
- A. **Brindley**, Mrs M. D.; 25, Madingley Road, Cambridge.
- E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
- E. **Brooks**, Prof. F. T., M.A., F.R.S.; Botany School, Cambridge.
- A. **Brown**, F. M.; Bryanccliffe, Hungerford Road, Huddersfield, Yorks.
- E. **Burges**, N. A.; Botany School, Cambridge.

- E. A. **Burt**, B. L.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Burt Davy**, Dr J.; Shotover Furze, The Ridings, Headington, Oxford.
- E. **Butcher**, R. W., B.Sc.; Fisheries Research Station, Alresford, Hants.
- A. **Buxton**, Prof. P. A.; London School of Hygiene, Keppel Street, London, W.C. 1.
- E. **de Caen**, Mrs. Ph.D.; Springfield, Dalgany, Co. Wicklow, Ireland.
- A. **Cameron**, A. E., D.Sc.; Dept. of Entomology, 10, George Square, Edinburgh.
- A. **Carey**, Miss E., Foxhill, Bracknell, Berks.
- A. **Carpenter**, Prof. G. D. Hale, M.B.E., D.M.; Penguelle, Hid's Copse Road, Cumnor Hill, Oxford.
- A. **Carpenter**, J. R., M.Sc.; 2670, N. Alpine Road, Grand Rapids, Michigan, U.S.A.
- A. **Carpenter**, Prof. K. E., Ph.D.; Zoology Dept., University of Liverpool.
- A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
- E. **Carter**, Dr Nellie; Armeria, Petersham Road, Richmond, Surrey.
- A. **Cawke**, E. M., 10, Algier's Road, Ladywell, London, S.E. 13.
- E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
- A. **Chapman**, Prof. R. N.; University of Hawaii, Honolulu, Hawaii.
- E. **Chapman**, V. J.; 13, Brookside, Cambridge.
- A. **Charteris**, Hon. Guy; 24, Oxford Square, London, W. 2.
- A. **Chitty**, D. H.; Bureau of Animal Population, University Museum, Oxford.
- E. **Clapham**, Dr A. R.; Botanical Dept., The University, Oxford.
- E. A. **Clements**, Prof. F. E.; Mission Canyon, Santa Barbara, California.
- A. **Colquhoun**, M. K.; Lane's End House, Woodlands St Mary, Newbury, Bucks.
- E. **Conway**, Miss V. M.; 61, De Freville Avenue, Cambridge.
- E. **Cooper**, Prof. W. S.; Dept. of Botany, University of Minnesota, Minneapolis, Minn.
- E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- A. **Corley**, H. V.; Hyron's Lodge, Amersham, Bucks.
- E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
- E. **Croydon Natural History and Scientific Society**, 27, High Street, Croydon.
- E. **Curtis**, Miss W. M., B.Sc.; 381, Holly Lodge Mansions, Highgate, London, N. 6.
- A. **Dalgety**, C. T.; Denver Hall, Downham Market, Norfolk.
- A. **Darling**, F. F., Ph.D.; Brae House, Dundonnell, by Garve, Wester Ross, Scotland.
- E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
- E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
- E. A. **Davis**, D. H. S.; Dept. of Public Health, Pretoria, S. Africa.
- E. **Davis**, T. A. W.; Forestry Station, Mozaruni, British Guiana.
- E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
- E. **Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
- A. **Diver**, C.; 40, Pembroke Square, Kensington, London, W. 8. (*Vice-President*).
- A. **Donaldson**, R. P.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.
- E. **Dowling**, Miss R. E., M.Sc.; The Nest, Ledgers Road, Slough, Bucks.
- A. **Duncan**, A. B., B.A.; Gilchristland, Closeburn, Dumfries.
- E. **Dundas**, J.; Chief Conservator of Forests, Ibadan, Nigeria.
- E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
- E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.
- E. **Edwards**, Miss D. A., 35, Queen's Gate Mews, Kensington, London, S.W. 7.
- E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
- E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
- A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.
- E. A. **Elton**, Charles; Bureau of Animal Population, University Museum, Oxford (*Hon. Editor of the Journal of Animal Ecology*).

- E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, Essex).
- E. **Evans, E. Price**; White Broom, 69, Westgate, Hale, Cheshire.
 - A. **Evans, F. C.**; Oriel College, Oxford.
- E. **Evans, G. C.**; Botany School, Cambridge.
 - A. **Eyre, Miss J.**; Dept. of Zoology, University of Cape Town, S.A.
- E. **Falk, P.**; 24, Rokeby House, Rugby.
- E. A. **Featherly, Prof. H. I.**; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.
- E. **Fenton, E. Wyllie, D.Sc.**; 13, George Square, Edinburgh.
 - A. **Fidler, J. H.**; Warrenside, Mapledurham, Reading.
- E. **Fisher, H. S., M.Sc.**; 35, Alexandra Road, Pietermaritzburg, Natal.
 - A. **Fisher, J. M. Mc.**; Zoological Society of London, Regent's Park, N.W. 8.
- E. A. **Fitzgerald, D. V.**; Clammer Hill, Haslemere, Surrey.
- E. **Foggie, A., B.Sc.**; c/o Conservator of Forests, Forestry Department, Accra, Gold Coast, Africa.
 - A. **Ford, J.**; Tsetse Research Dept., Shinyanga, Tanganyika Territory.
- E. **Fraser, G. K., M.A., D.Sc.**; Macaulay Institute, Craigiebuckler, Aberdeen.
 - A. **Freeman, R.**; Magdalen College, Oxford.
- E. **Fritsch, Prof. F. E., F.R.S.**; Pilgrim's End, West Humble, Dorking.
- E. **Fuller, Prof. G. D.**; Botany Dept., The University, Chicago, Ill., U.S.A.
- E. **Galloway, J. A.**; Oak Bank, Bowness on Windermere, Westmorland.
- E. **Gams, Dr H.**; Innsbruck-Hotting, Schreeburggasse 67, Austria.
 - Garland, R. H. C.**; 21 Brading Av., Southsea, Hants. (*Associate member*).
- E. A. **Garner, J. H., B.Sc.**; West Riding Rivers Board, 71, Northgate, Wakefield.
- E. **Gibson, Miss C. M.**; The Municipal College, Portsmouth.
- E. **Gilbert-Carter, H., M.A., M.B.**; Cory Lodge, Botanic Garden, Cambridge.
- E. **Gillman, H., M.Sc.**; District Agricultural Office, Bukoba, Tanganyika Territory.
- E. **Gilmour, J. S. L., B.A.**; Royal Botanic Gardens, Kew, Surrey.
- E. A. **Glasgow and Andersonian Nat. Hist. and Microscopic Soc.**; Societies' Rooms, Royal Technical College, Glasgow.
- E. A. **Godwin, H., Ph.D.**; Botany School, Cambridge (*Hon. Secretary*).
- E. A. **Good, R. D'O.**; University College, Hull.
- E. **Gourlay, W. B., M.A., M.B.**; 7, Millington Road, Cambridge.
- E. **Griffith Tedd, H.**; P.O. Box 30, Xanthie, Greece.
- E. A. **Griffiths, B. M., D.Sc.**; Dept. of Botany, University Science Labs., South Road, Durham.
 - A. **Gurney, Dr R.**; Bayworth Corner, Boar's Hill, Oxford.
- E. **Halket, Miss A. C., B.Sc.**; Bedford College, Regent's Park, London, N.W. 1.
- E. **Halliday, W. E. B.**; c/o Dominion Forest Service, 813, New Federal Building, Winnipeg, Manitoba, Canada.
- E. A. **Hancock, G. L. R.**; Makenene College, Box 262, Kampala, Uganda.
- E. **Hanson, Dr Herbert C.**; Botanist and Head of Dept. of Botany, North Dakota Agric. College and Expt. Station, Fargo, North Dakota, U.S.A.
 - A. **Hardy, Prof. A. C., M.A.**; University College, Hull (*Vice-President*).
- E. **Hare, C. Leighton, B.Sc.**; Department of Botany, The University, Aberdeen.
 - A. **Hare, Prof. T., M.D.**; 70, Holywell Hill, St Albans.
- E. **Harley, J. H.**; University Dept. of Botany, High Street, Oxford.
- E. **Harris, C. M.**; Forest Office, Entebbe, Uganda.
 - A. **Harris, W. V.**; Dept. of Agriculture, Morogoro, Tanganyika Territory.
- E. **Harrison, A. B.**; The Hollies, Farndon, Newark-on-Trent.
 - A. **Hartley, C. H., B.A.**; Eton College, Windsor, Bucks.

- A. **Harvey**, A. L., M.Sc.; Dept. of Zoology, University College of S.W. England, Exeter, Devon.
- E. **Heddle**, R. G., M.A., B.Sc.; Edinburgh and E. of Scotland College of Agric., 13, George Square, Edinburgh.
- E. A. **Heslop Harrison**, Prof. J. W.; Dept. of Botany, King's College, Newcastle-upon-Tyne.
- E. **Hewetson**, C. E.; Indian Forestry Service, Jubbulpur, Central Provinces, India.
- E. **Hilary**, Miss D., B.Sc.; 15, Plevna Terrace, Bingley, Yorks.
- E. **Hill**, Sir A. W., F.R.S.; Royal Botanic Gardens, Kew, Surrey.
- E. **Hill**, Prof. T. G.; University College, London, W.C. 1.
- A. **Hobby**, B. M., M.A., D.Phil.; University Museum, Oxford.
- A. **Hodgkin**, E. P.; Institute for Medical Research, Kuala Lumpur, F.M.S.
- E. **Holch**, Dr A. E.; Botany Dept., University of Denver, Colorado, U.S.A.
- E. **Hole**, D. R., B.Sc.; Rousdon, Cutbush Lane, Shinfield, Reading.
- E. **Holtum**, R. E., M.A.; The Botanic Gardens, Singapore.
- E. **Hope Simpson**, J. F.; University Dept. of Botany, Oxford.
- E. **Horne**, F. R.; Seale-Hayne Agric. College, Newton Abbot, Devon.
- E. **Howarth**, W. O.; Botany Dept., The University, Manchester.
- E. **Hubbard**, C. E.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
- E. **Hughes**, R. E.; School of Agriculture, University College, Bangor.
- E. **Hugh-Jones**, P.; King's College, Cambridge.
- A. **Hume**, Capt. C. W.; 284 Regent's Park Road, Finchley, London, N. 3.
- A. **Huntingdon**, E.; Dept. Geological Sciences, 4, Hillhouse Avenue, New Haven, Connecticut, U.S.A.
- E. **Hutchinson**, R. R.; 11, Fryston Avenue, Croydon.
- E. **Hyde**, H. A., M.A.; National Museum of Wales, Cardiff, S. Wales.
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STUDIES ON THE VEGETATION OF MAURITIUS

II. THE EFFECT OF ENVIRONMENT ON CERTAIN
FEATURES OF LEAF STRUCTURE

BY R. E. VAUGHAN AND P. O. WIEHE

*Royal College, Mauritius**(With four Figures in the Text)*

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I. INTRODUCTION

ALTHOUGH considerable information has been collected in connexion with the effect of environmental factors upon the structure of individual plants in different communities, little is known of the variation under natural conditions existing in the same species growing in different habitats.

In a previous paper on the Vegetation of Mauritius (Vaughan & Wiehe, 1937) it was shown that the distribution of the indigenous and exotic communities of the island was primarily affected by the climate, and two broad zones could be distinguished, namely, the wet upland region, and the relatively drier lowland localities. An interesting feature of the native communities is that many species are common to both regions, and the purpose of this paper is to investigate quantitatively the extent of variation of certain factors exhibited by these species.

It is evident that an almost unlimited number of variants are available for study, from morphological features often employed for systematic classification to various anatomical characters such as shape and size of palisade cells, thickness of epidermis, and many others (Zalenski, 1904, quoted by Maximov, 1929).

Further, more precise information is likely to be obtained by the study of the variation of a few factors in a number of species rather than attempting to study a large number of factors in one species only.

Nine species have been selected for this investigation, and the factors to be studied have been restricted in the first instance to a few in which accurate

numerical data could easily be obtained. These are: mean length and area of leaves, and area and frequency of stomata and lower epidermal cells. In addition certain features susceptible to variation such as general morphology of leaves, including heterophylly, and leaflet frequency have been noted.

Climate

A general descriptive account of the climate illustrated by diagrams showing the magnitude of some more important meteorological elements has already been published (Vaughan & Wiehe, 1937). More exact information is presented in Table I where eight elements are given, the figures for the same element in the two different localities being shown for comparison in adjacent columns.

The main feature of the temperature is its uniformity. There is a difference of 3.1° C. (5.6° F.) in mean yearly temperatures; the mean range is small, in each case being 5.5° C. (8.9° F.) in the uplands and 7.5° C. (13.5° F.) in the lowlands. The mean temperature of the hottest month, February, only exceeds that of the coolest month, August, by 6.0–6.5° C. (10.8–11.7° F.) in both localities.

Striking differences exist between the two rainfalls, that of the uplands being 2514 mm. (99 in.) greater than the lowlands. In this connexion, however, it should be noted that the mean duration of sunshine in the lowlands only exceeds the uplands by a little less than 1 hr. This is partly due to the fact that during the heavy afternoon summer rains the sun is often obscured in both regions, while heavy rain is falling only in certain isolated areas of the uplands. It is in the winter months, the season for orographic rains, that the uplands receive at least four times as much rain as the lowlands; and although the latter experiences a "dry" cool season from June to November, yet the mean number of rain days is never less than 12 per month. Relative humidity is 12 units less in the lowlands, whereas the value for mean saturation deficit, a better index of the hygrometrical state of the atmosphere as it affects the plant, is 2.8 mb. in the uplands and 6.7 in the lowlands.

A summary of the quantitative difference in some of the meteorological elements is given by the following figures, which represent the amount by which the uplands value is greater or less than the lowlands:

Mean max. temp. ° C.	Mean min. temp. ° C.	Mean temp. ° C.	Mean range ° C.	Rela- tive humi- dity	Satura- tion deficit mb.	Rainfall mm.	Rain days	Sunshine hr.	Wind vel. metres per sec.
-3.1	-2.1	-3.1	-2.2	+12	-3.9	+2514	+57	-0.83	+0.9

Soils

The soil types of the localities selected probably do not differ enough in their physical properties to have an effect on the factors investigated; they are still immature and very porous, outcrops of unweathered lava are common and large stones and boulders are typical features. On the other hand their chemical

properties differ widely, owing to the extent of laterization to which they have been subjected, the upland type being highly laterized and more acid than the lowland type in which less leaching has occurred.

II. SPECIES INVESTIGATED AND METHODS

(a) *Species investigated*

It was desirable in choosing the species required for this investigation that they should be representative of the different strata of the forest complex and that they should be common enough in both localities to enable sampling to be easily and effectively carried out. Owing to the very scanty remnants of indigenous vegetation, particularly in the lowlands, these desiderata were not easily achieved. The material representing the lowland regions was obtained from a spur of the Tamarin Mountain near Yemen in the Black River district, 200 ft. above sea-level and on Plaine des Roches (75 ft.) in the district of Flacq. The climate in these localities differs somewhat from that of the Royal Alfred Observatory, Pamplémousses (Table IB), Black River being less humid and Plaine des Roches having a slightly higher rainfall.

In the uplands the material was gathered in the climax forest of Macabé and in the indigenous thickets of Perrier near the Mare aux Vacoas. The climate in both these areas agrees fairly well with that of the Royal College, Curepipe, some elements of which are given in Table I, A 1-A 5.

Nine species were finally selected, in seven of which the same species occurred both in the uplands and lowlands. The remaining two genera are represented by two species each, one in each locality. In both these cases, however, it is probable that the two species are merely climatic variants.

The genera and species chosen may now be enumerated. The enumeration follows the same order as that given in the summary of results (Table II, p. 267) where their world distribution will also be found.

(1) *Elaeodendron orientale* Jacq. (Celastraceae), Bois d'Olive. A large tree, dominant in the open canopy of the lowland forest. It displays the same habit in the uplands but is much less frequent. The interest of this species lies in its remarkable heterophyllous character and has been chosen in order that the variations in leaf form under different climatic conditions prevailing in the two localities might be studied.

(2) *Mimusops petiolaris* Dubard (Sapotaceae), Bois de Makak. This is the "red ebony" of the early Dutch settlers and one of the commonest species of the canopy both in the uplands and lowlands.

(3) *Ludia sessiliflora* Lam. (Flacourtiaceae), Bois mozambique and (4) *Fernelia buxifolia* Lam. (Rubiaceae), Bois buis, are both second, closed, stratum species. *Fernelia* was chosen as a trial species to determine the most suitable methods of sampling and to illustrate variation in individuals as opposed to aggregates.

Table I. *Monthly and yearly normals of various meteorological elements*

Month	1		2		3		4		5		6		7		8		9	
	Mean max. temp. °C.		Mean min. temp. °C.		Mean range °C.		Mean temp. °C.		Mean relative humidity		Mean monthly rainfall mm.		Rain days		Mean sunshine hours/day		Mean wind velocity metres/sec.	
	A	B	A	B	A	B	A*	B	A	B	A	B	A	B	A	B	A†	B
January	25.9	29.8	20.8	22.6	5.1	7.2	23.1	25.9	87.1	76	525.4	215.4	22	20	6.50	7.73	3.1	2.5
February	26.4	29.5	20.3	22.8	6.1	6.7	23.1	25.8	89.3	79	403.6	197.0	23	19	7.04	7.60	3.3	2.3
March	25.3	28.9	20.4	22.3	4.9	6.6	22.6	25.2	90.2	80	436.2	220.4	24	20	6.95	7.15	3.2	2.4
April	24.2	27.6	19.0	21.1	5.2	6.5	21.3	24.1	89.9	80	438.4	126.4	25	17	6.50	7.55	3.6	2.7
May	21.4	25.9	17.2	19.1	4.2	6.8	19.0	22.2	90.5	78	296.1	90.4	23	16	7.09	7.39	3.7	2.8
June	20.9	24.4	15.4	17.0	5.5	7.4	18.1	20.5	87.1	76	184.8	64.9	21	16	7.20	7.48	4.1	3.0
July	19.8	23.7	14.5	16.5	5.3	7.2	16.9	19.8	89.0	76	232.2	59.6	26	19	7.09	7.57	4.0	3.4
August	19.8	23.9	14.0	16.5	5.8	7.4	16.6	20.0	88.4	74	291.7	62.5	25	18	6.89	7.57	4.9	3.5
September	20.3	25.1	14.5	17.0	5.8	8.1	17.1	20.8	84.7	72	104.6	35.3	19	15	6.97	7.98	4.5	3.3
October	21.7	26.8	15.6	18.0	6.1	8.8	18.4	22.1	82.7	70	127.4	40.4	17	14	7.42	8.18	3.8	2.8
November	24.0	28.4	17.5	19.6	6.5	8.8	20.5	23.7	81.4	69	240.8	44.6	15	12	7.13	8.80	3.3	2.6
December	25.4	29.7	19.0	21.6	6.4	8.1	21.9	25.3	82.5	73	510.7	116.1	20	17	6.64	8.35	3.0	2.5
Mean year	22.9	27.0	17.4	19.5	5.5	7.5	19.9	23.0	86.9	75	3791.9	127.8	260	203	6.95	7.78	3.7	2.8
Period	1930	1891	1930	1891	1930	1891	1930	1876	1922	1891	1922	1888	1922	1888	1925	1887	1930	1876
	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to
	1937	1930	1937	1930	1937	1930	1937	1930	1926	1930	1926	1930	1926	1930	1934	1930	1934	1930

* Mean temperature obtained from 0.5 (max. + min.) - 0.3 °C.; probably does not differ by more than ±0.1 from mean temperature from hourly values.

† 10 a.m. values + 8%, this being the excess of mean value for the day over the 10 a.m. value at the Observatory.

Table II

A = Uplands. B = Lowlands.

Life form	Species, Family and Distribution	1		2	3		4		5	6		
		Leaf area sq. cm.			Leaf area ratio A/B	Leaf length cm.		Stomata per sq. mm. (with standard deviations)		Stomata number ratio A/B	Stomata per leaf	
		A	B	A		B	A	B	A		B	
Leaves simple:	1. <i>Elaeodendron orientale</i> Jacq., Celastraceae, R., Rod.	21.7	18.5	1.17	5.9	6.2	327 ± 6.0	394 ± 9.0	67 ± 10.8	0.83	709,590	728,900
	2. <i>Mimusops petiolaris</i> Dubard, Sapotaceae, E.	54.7	46.8	1.16	8.9	7.8	108 ± 1.5	174 ± 4.5	66 ± 4.8	0.64	590,760	814,320
	3. <i>Ludia sessiliflora</i> Lam., Flacourtiaceae, R. Sey., Rod., E. Africa	13.3	3.3	4.07	5.9	3.3	480 ± 10.5	837 ± 39.0	357 ± 40.3	0.57	638,400	276,210
	4. <i>Fernexia buxifolia</i> Lam., Rubiaceae, Rod.	5.1	1.5	3.40	2.7	1.3	269 ± 7.5	474 ± 10.5	205 ± 13.0	0.56	137,190	71,100
	5. <i>Scutia Commersoni</i> Brong., Rhamnaceae, R.	9.1	5.5	1.66	3.8	2.7	376 ± 9.0	583 ± 16.5	207 ± 18.8	0.65	342,160	320,650
Leaves compound:	6. <i>Doratoxylon mauritianum</i> Thouars, Sapindaceae, R.	15.0	4.3	3.52	5.6	3.1	584 ± 9.0	782 ± 12.0	198 ± 15.0	0.75	876,000	336,260
	7. <i>Protium obtusifolium</i> March., Burseraceae, E.	32.4	25.5	1.27	8.0	7.9	254 ± 6.0	308 ± 4.5	54 ± 7.5	0.83	822,960	785,400
	Different species:											
8. <i>Conopiarquia mauritiana</i> (Poir) R.E.V., Apocynaceae, R.		41.5	—	—	8.8	—	69 ± 3.0	—	—	—	286,350	—
	9. <i>C. persicariifolia</i> (Jacq.) R.E.V., Apocynaceae, R.	—	24.1	1.72	—	10.9	—	73 ± 3.0	4 ± 4.2	0.95	—	175,980
	10. <i>Erythroxylon laurifolium</i> Lam., Linaceae, R.	14.1	—	—	5.6	—	143 ± 4.5	—	—	—	201,630	—
	11. <i>Erythroxylon</i> sp., Linaceae, R.	—	10.6	1.33	—	5.1	—	256 ± 7.5	113 ± 8.5	0.56	—	271,360
Means		22.9	15.6	2.14	6.1	5.4	290 ± 6.0	431 ± 12.0	141 ± 13.5	0.71	511,671	420,014

Life form	Species, Family and Distribution	Area of one		Stomata		Percentage area		Epidermal cells		Epi-dermal		Stomatal index	
		sq. mm. × 10 ⁻⁴		ratio	of leaf covered by stomata		per sq. mm.	number	ratio	cell area		S + E	
		A	B		A	B				A/B	S + E	A	B
Leaves simple:	1. <i>Elaeodendron orientale</i> Jacq., Celastraceae, R., Rod.	45.2	436.8	1.04	14.88	17.19	3650	3711	0.98	229	223	1.03	8.2
	2. <i>Mimusops petiolaris</i> Dubard, Sapotaceae, E.	1027.0	656.0	1.56	11.09	11.46	3707	4222	0.88	239	210	1.14	2.8
	3. <i>Ludia sessiliflora</i> Lam., Flacourtiaceae, R. Sey., Rod., E. Africa	384.5	336.5	1.11	18.55	28.12	3110	3634	0.85	262	198	1.32	1.3
	4. <i>Fernexia buxifolia</i> Lam., Rubiaceae, Rod.	221.9	219.7	1.01	5.97	10.41	3637	3248	0.93	322	274	1.18	8.0
	5. <i>Scutia Commersoni</i> Brong., Rhamnaceae, R.	292.2	264.1	1.10	10.97	15.39	4291	4364	0.98	207	194	1.07	8.1
	Leaves compound:												
	6. <i>Doratoxylon mauritianum</i> Thouars, Sapindaceae, R.	164.6	159.2	1.03	9.61	12.33	4618	4499	1.02	196	195	1.00	11.2
Different species:	7. <i>Protium obtusifolium</i> March., Burseraceae, E.	538.4	525.5	1.02	13.45	16.19	2136	2165	0.99	404	387	1.06	10.6
	8. <i>Conopiarquia mauritiana</i> (Poir) R.E.V., Apocynaceae, R.	821.9	—	—	5.68	—	2875	—	—	327	—	2.4	—
	9. <i>C. persicariifolia</i> (Jacq.) R.E.V., Apocynaceae, R.	337.6	—	—	4.82	—	1804	—	—	593	—	8.2	—
	10. <i>Erythroxylon laurifolium</i> Lam., Linaceae, R.	—	310.1	1.00	—	7.96	—	2346	0.68	—	393	1.35	9.8
	11. <i>Erythroxylon</i> sp., Linaceae, R.	471.7	406.2	1.12	10.6	13.83	3225	3469	0.92	309	264	1.13	6.7
	Means												

Abbreviations

Life forms: Mz = α Mesophanerophyte, 15 m. and above.

Mb = β Mesophanerophyte 8–15 m.

Mi = Microphanerophyte 2–8 m.

L. = Liane.

Distribution: E. Endemic.
R. Réunion.
Rod. Rodriguez.
Sey. Seychelles.

(4) *Scutia Commersoni* Brong. (Rhamnaceae), "Liane Bambaras", a woody liane with slender thorny branches was selected as a representative of this life form; it is occasional in both localities.

(5) *Doratoxylon mauritianum* Thouars (Sapindaceae), "Bois de Sagaie rouge". In the lowlands this species is a co-dominant component of the second stratum of the climax forest; it is less common in the uplands. It also possesses marked heterophylly especially in lowland forms, but of a different type from that found in *Elaeodendron*.

(6) *Protium obtusifolium* March. (Burseraceae), "Bois colophane bâtard". A medium-sized balsamiferous tree with compound leaves common in the lowlands. It does not seem to have been able to establish itself in the upland forests and is seldom found far from the vicinity of stream banks.

The genera represented by two species, one in each habitat are (8) *Conopharyngia* (Apocynaceae) and (9) *Erythroxylon* (Linaceae). *Conopharyngia mauritiana* (Poir) R.E.V., "Bois de lait", is dominant in the third stratum of the upland climax forest and thrives under conditions of extreme shade and uniform humidity. *C. persicariifolia* (Jacq.) R.E.V. occurs in the indigenous thickets of the lowlands, usually somewhat exposed conditions. *Erythroxylon* spp., "Bois ronde or Bois piment", are very common in the earlier phases of development of both lowland and upland forests.

The great diversity of form displayed by these species even in the same locality and still greater range of variation which becomes apparent under different climatic conditions, has resulted in a confused nomenclature. This has been accentuated by the fact that the early systematists, Lamark, Poivre and de Candolle, were liberal with specific names which were freely bestowed on individuals described from a few herbarium sheets. On the other hand, when the *Flora of Mauritius* was written (Baker, 1877), species, varieties and climatic types were indiscriminately lumped together. The present investigation may serve to emphasize the fact that the study of a large number of individuals in the field is essential if the proper taxonomic status of the species is to be elucidated.

(b) Methods

The great variation of one of the factors to be determined, namely stomatal frequency, is well known. Considerable differences have been found in stomatal frequency by several workers according to the region of the leaf examined, sun and shade aspects, position of leaf on plant and many other factors (Yapp, 1912; Maximov, 1926; Salisbury, 1927). It was important therefore that a suitable method of sampling should be used which would serve to eliminate variation of this nature and to obtain, in the first instance, a good average value for the individual plant. In the method finally adopted, 250 leaves were picked at random; from these fifty were selected and ten random counts of stomatal frequency made on each leaf. This yielded a total of 500 individual values for stomatal frequency per field. From a study of the normal distribution curves

(and the standard deviations obtained) it was evident that this method was truly random and that the variations referred to above had been eliminated. The species *Fernelia buxifolia* was found to be suitable for a preliminary investigation on the methods of sampling. Further, the results obtained could be used to indicate in some measure the nature and extent of variation between individuals in the same locality. Four individuals were selected at random in the uplands and four in the lowlands and the stomatal frequency and leaf length determined in each case, using the method of sampling already described. The mean stomatal frequency and leaf length of each of the eight individuals was thus obtained and their standard deviations calculated. The normal distribution curves for the stomatal frequency and leaf length of these eight species are shown in Fig. 4 and will be discussed later.

For the main investigation, however, variation in different habitats only was studied by selecting the required number of leaves from twenty-five individuals in the case of *Ludia*, *Scutia*, *Doratoxylon* and *Erythroxylon*, and from twelve individuals of *Elaeodendron*, *Mimusops*, *Protium* and *Conopharyngia*.

Determination of factors investigated.

(i) *Stomatal frequency.* Epidermal strips were cut at random from the selected leaves, stained in methylene blue, differentiated in acid alcohol and mounted in glycerol. The collodion method was found to be unsatisfactory. To avoid shrinkage or distortion the leaves were fixed in alcohol as soon as possible after gathering. Ten counts were made on strips prepared from each leaf using a $\frac{1}{8}$ in. objective and counting the number of stomata visible in the whole field, the area of which was 0.04052 sq. mm. In every case the standard deviations and normal distribution curves for a series of counts were determined in order to ascertain the nature and extent of variation.

(ii) *Area of stomata.* The area of stomata was determined by measuring the length and breadth of the guard cells when closed, using an eyepiece micrometer. The area of the stoma was calculated on the assumption that it was elliptical in shape.

(iii) *Frequency and area of lower epidermal cells.* These determinations were made on material prepared for stomatal frequency. A micro-projector with a $\frac{1}{8}$ in. objective was found to be suitable for epidermal cell counts, a projection being made on to a sheet of paper of known area. In this way large numbers of epidermal cells could be quickly counted. In addition the number of stomata could be checked and compared with the values obtained by direct vision using the method described above. The area of the epidermal cells (Table II, col. 12) may also be calculated from the following expressions using the data already obtained:

$$\text{Area of epidermal cells} = \frac{1 - \text{area covered by stomata per sq. mm.}}{\text{Number of epidermal cells per sq. mm.}}, \quad (1)$$

Area of epidermal cells

$$= \frac{X - [\text{Number of stomata in } X \text{ sq. mm.} \times \text{area of 1 stoma}]}{\text{Number of epidermal cells in } X \text{ sq. mm.}}, \quad (2)$$

where X = area of field.

The difference between the values obtained using these two expressions was of the order of 5%.

(iv) *Leaf length and area.* The method of sampling was the same as that employed in obtaining the material for stomatal frequency. Leaf lengths were measured without the petiole and in compound leaves the leaflet was taken as the unit. The mean area was measured by weighing 100–250 leaves and then determining the weight of 50–100 known areas removed from the leaves by a cork borer. In addition to the determinations already described, a further factor was studied in the two species having compound leaves. This was the leaflet frequency per leaf in each locality. These results are based on counts obtained from 500 leaves selected at random from twenty-five individuals.

III. PRESENTATION OF RESULTS

The general summarized results are shown in Table II, in which the family, life form and distribution of the species are given. The figures from each locality are represented side by side in each column so that the effect of environment can be readily compared. From the experimental results obtained, the ratios for leaf area, stomatal and epidermal cell frequency, area of stomata and epidermal cells in the two localities have been calculated. These figures are given in cols. 2, 5, 11, 8 and 13. From the experimental values of leaf area (col. 1) and stomatal frequency (col. 4) the total number of stomata per leaf (col. 6) has been determined. The area of the stomata being known (col. 7) the percentage area of leaf covered by stomata may be calculated (col. 9). In addition the "stomatal index" for the nine species, as defined by Salisbury (1927), is shown in col. 14.

The results obtained for *Fernelia buxifolia* are given in Table III and expressed graphically in Fig. 4.

Table III

Individual	Leaf length (cm.) and standard deviations		Stomatal frequency (number per sq. mm.) and standard deviations	
	Uplands	Lowlands	Uplands	Lowlands
1	2.2 ± 0.063	1.4 ± 0.024	265.1 ± 11.4	475.1 ± 12.3
2	2.3 ± 0.063	1.3 ± 0.022	238.6 ± 7.1	470.1 ± 8.6
3	2.9 ± 0.071	1.2 ± 0.022	215.6 ± 2.3	488.0 ± 11.0
4	3.5 ± 0.094	1.1 ± 0.025	354.8 ± 9.3	460.7 ± 11.0
Means	2.7 ± 0.073	1.3 ± 0.023	268.5 ± 7.5	473.5 ± 11.0
Coefficient of variability*	2.67	1.85	2.90	2.25

* Coefficient of variability = $\frac{\text{Standard deviation}}{\text{Mean}} \times 100$, i.e. the percentage standard deviation of the mean.

The mean figures for this species as well as the other factors determined are given in the general table of results. These figures are not intended to show whether correlation exists between stomatal frequency and size of leaf in the same locality but may be used to compare the amplitude of variation of two arbitrarily chosen factors between individuals in the uplands and those in the lowlands.

For the species *Doratoxylon* which has compound leaves, the frequency of leaflet per leaf has been investigated, the counts extending over five hundred leaves in each case. The results are given below and are expressed graphically in Fig. 1.

Leaflets	1	2	3	4	5	6	7	8	9	10	11	12	13
Number of leaves:													
Uplands	1	105	60	287	14	33	—	—	—	—	—	—	—
Lowlands	—	6	6	76	27	164	42	140	14	20	1	3	1

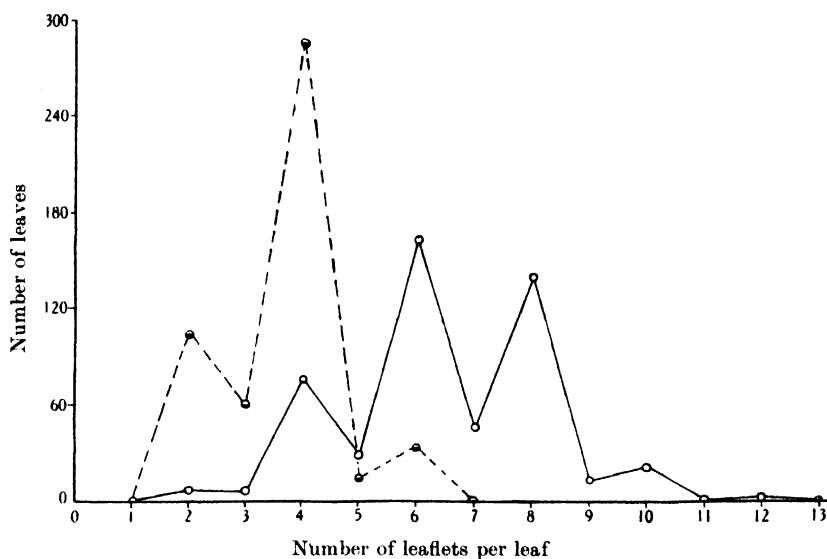


FIG. 1. Variation in leaflet number per leaf in *Doratoxylon mauritianum* Thouars in the uplands (broken lines) and the lowlands (continuous lines). Based on five hundred leaves selected at random from twenty-five individuals in each locality.

IV. DISCUSSION

(a) Leaf morphology

It is of course evident that environment would have a profound influence on the morphology of the species investigated and it was expected that the area and shape of the leaf would be markedly modified according to the habitat of the species. A quantitative study of the nine species does however reveal some points of interest.

The variation in leaf length and area is given in cols. 1, 2 and 3 of Table II

in which it may be seen that the leaf area and in most cases leaf length are considerably increased under moist conditions. This increase reaches a maximum in the species *Ludia*, the upland leaves (13.3 sq. cm.) being four times larger than those of the lowlands (3.3 sq. cm.). The mean increase in area for the nine species taken as a whole is over 75%.

The increase in area of the lamina is effected in several ways and the following types of modifications in leaf form may be distinguished:

(1) Increase in length of both axes of the leaf. The leaf retains the same shape but a considerable increase in both length and breadth may take place. Two genera may be included here, namely, *Fernelia* and *Scutia*.

(2) The shape of the leaf changes from lanceolate to ovate or obovate. The difference in shape is more extreme in some cases than in others (Fig. 2). It may be noticed that the change in shape is more significant than the change in area, for in some individuals of *Elaeodendron* it was observed that the obovate form was smaller in area than the oblong lowland form. The significance of this fact becomes clear when the heterophylly of the species is understood. This type of change includes the majority of the species studied: *Ludia*, *Protium*, *Conopharyngia*, *Erythroxylon* and *Elaeodendron*.

(3) The modification in the leaf of *Mimusops*, a top canopy species, is largely due to changes in the petiole. As more humid conditions prevail, the petiole decreases in length and at the same time becomes much thicker. The leaf in the uplands is also more coriaceous, with the result that a very different habit is observed in the two localities, lowland species having more or less drooping leaves with slender petioles while in the uplands the leaves are rigid and in stiff whorls at the ends of the branchlets.

(4) A peculiar change is observed in the case of *Doratoxylon*, a species with compound leaves. The leaflets in the lowlands are usually six to ten in number, subequal, or with the uppermost pairs slightly larger. As the rainfall increases, the number of leaflets becomes reduced, most commonly in pairs (Fig. 1), and at the same time the increase in size of the terminal pair of leaflets becomes much more pronounced. In extreme cases the leaflets are reduced to a single pair, a form which was formerly given specific rank as *Melicocca diphylla* Bojer (Fig. 2(3)).

Heterophylly. The variation in leaf area and form under different climatic conditions is evidently closely connected with heterophylly. The remarkable heterophylly exhibited by a large number of Mascarene species has already been noticed by Balfour (1879) who recognized three types:

(i) The leaves on the young plant are the same shape as the mature leaves but are much smaller and sometimes possess spinous margins: for example *Fernelia* and *Scutia*.

(ii) The "juvenile" leaf is linear or lanceolate, usually longer than the mature leaf and sometimes exceeding the latter in area. This is a very common type of heterophylly and is well displayed in *Elaeodendron* (Fig. 2(7)).

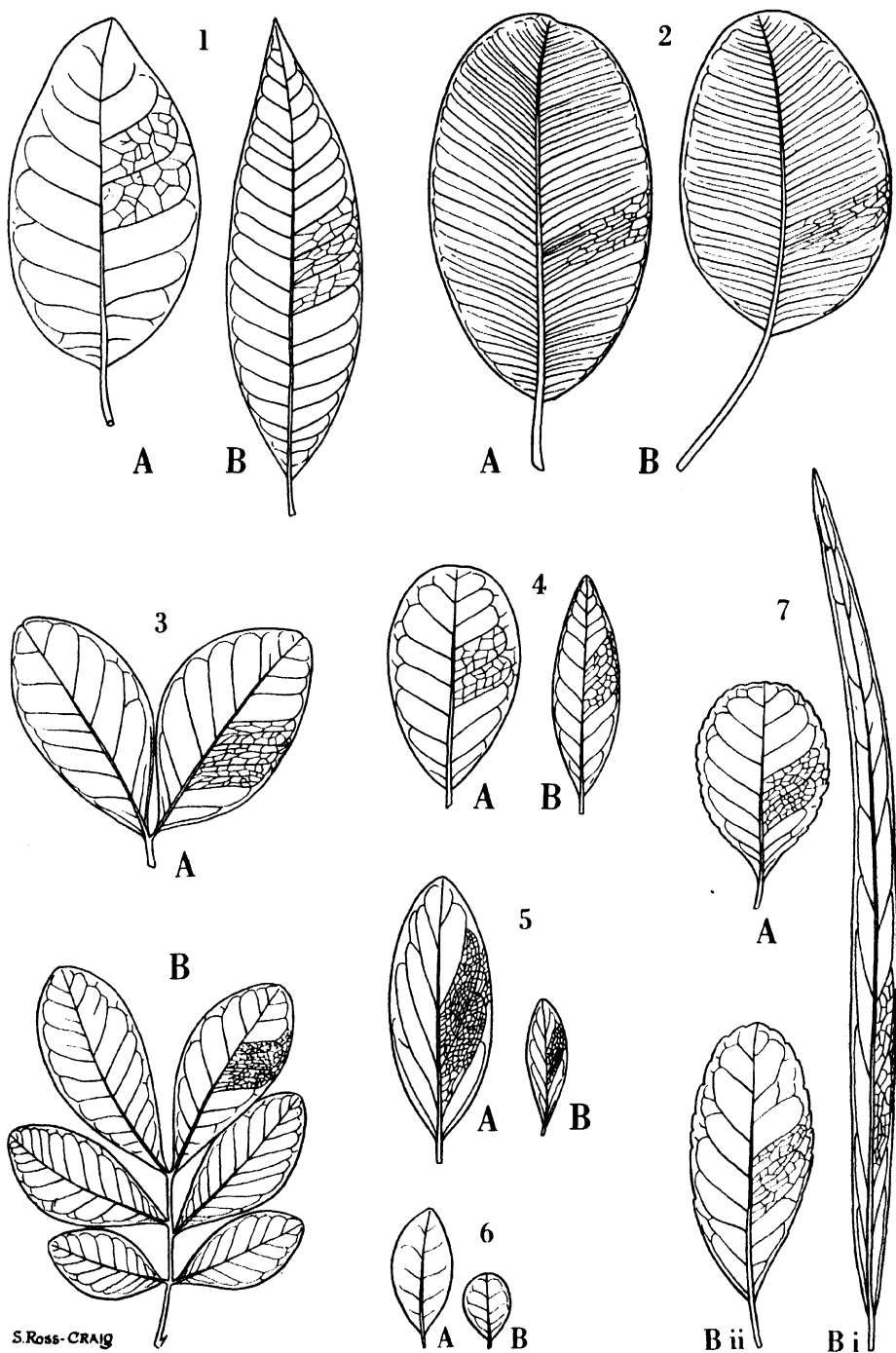


FIG. 2. Upland (A) and lowland (B) leaves of (1) *Conopharyngia*, (2) *Mimusops petiolaris* Dubard, (3) *Doratoxylon mauritianum* Thouars, (4) *Erythroxylon*, (5) *Ludia sessiliflora* Lam., (6) *Fernelia buxifolia* Lam., (7) *Elaeodendron orientale* Jacq. B i, leaf from coppice shoot or young plant; B ii, transitional type of leaf common in lowlands. $\times \frac{1}{2}$.

(iii) Unequal development of the lamina takes place, the shape of the juvenile leaf depending largely on the disposition of the main veins. If these are parallel or pinnate a pinnatifid leaf is formed. Palmate leaves are produced when the secondary veins are few in number and either alternate or branch away from the midrib at a short distance beyond the base of the leaf.

To these three types a fourth may be added:

(iv) In certain species with compound leaves, the juvenile leaves possess more leaflets, which at the same time become much smaller. This modification is well seen in *Doratoxylon*.

A curious feature of Mascarene heterophylly is that it may vary from species to species. For example, the heterophylly of *Clerodendron heterophyllum* R.Br. from Mauritius belongs to type (ii) above, whereas the Rodriguez species *C. laciniatum* Balf. has a palmate juvenile leaf.

It is clear that in many cases the change in leaf form exhibited by a species in passing from the lowlands to the uplands is merely a continuation of the change from juvenile to mature leaves displayed in heterophylly. Thus in *Doratoxylon* we have the sequence: leaflets numerous (juvenile leaves of the lowlands) → leaflets six to ten (mature leaves of the lowlands) → leaflets two to six (mature leaves of the uplands). In other species the sequence is: linear juvenile leaves in the lowlands → lanceolate mature leaves in the lowlands → ovate or obovate leaves in the uplands. Further it is significant that the form of heterophylly described above is much rarer in the uplands; sometimes the juvenile leaves are the same shape but larger than the mature leaves, probably a shade factor due to the very low light intensity in the upland forests.

These observations seem to indicate that the heterophylly displayed in the lowlands may be regarded as a xeromorphic character; it is important to point out, however, that it is not always a simple reduction in leaf area which is achieved, for the juvenile leaf of *Elaeodendron* is often two or three times larger than the mature leaf (Fig. 2(7)). The practical consequence of heterophylly is that the distance of any particular portion of the mesophyll from a principal vein is reduced, in other words the irrigating system of the leaf is relatively increased.

The leaf morphology of *Mimusops petiolaris* is an interesting example which may be cited in support of this interpretation of heterophylly. The study of this species reveals certain evidently correlated facts: heterophylly is not marked, the difference in area of the leaves in the moist and dry localities is small, and the upland leaves are ovate-oblong whereas those of the lowlands tend to become orbicular—the reverse of all other species investigated. In this particular species, however, it is seen that a very efficient irrigating system is already present in the form of a large number of closely ranked parallel secondary veins.

There is, however, conflicting evidence as to the nature of the connexion, if any, between heterophylly and the water relations of the plant. In young or

coppiced *Elaeodendrons* the heterophylly is most marked in leaves near the ground and becomes progressively less evident towards the apex of the tree, that is, as the distance from the water supply increases. In most of the Australian eucalypts, the youth leaves are round or ovate and those of the mature plant lanceolate, a character which persists in species of this genus introduced into Mauritius even in trees planted in the uplands.

(b) *Stomata and lower epidermal cells*

The work of a number of authors (Yapp, 1912; Maximov, 1929; Salisbury, 1927) has shown that certain xeromorphic features exhibited by plants growing under dry conditions are such as to increase transpiration and thereby facilitate irrigation of the leaf. The analysis of the figures concerning stomatal and lower epidermal cell frequencies and areas further emphasize this point. It is found that in all cases examined, the number of stomata per unit area is much higher under dry conditions (Table II, col. 4). This increase in frequency may be gauged by the fact that 70,403 stomata were counted in upland individuals and 107,007 in lowland individuals, the area over which the counts were made being the same in each case. The increase in stomatal frequency, however, varies within wide limits from 10% in *Mimusops petiolaris* to 84% in *Fernelia buxifolia*.

The stomatal frequency of the nine species under the same climatic conditions is of interest owing to its very great variation and the apparent absence of correlation between frequency and life form. Eight of the species chosen for this investigation are phanerophytes which may be conveniently grouped into different height classes. In the lowlands the highest frequency recorded was 837 stomata per sq. mm. in *Ludia sessiliflora*, a micro-phanerophyte 2–8 m. high, while in the same station the frequency of *Conopharyngia persicariifolia*, belonging to the same height class, the frequency falls to 73. On the other hand, *Mimusops petiolaris*, which is a dominant species of the climax canopy and often attains a height of 35 m., has a frequency of only 174. In this respect the results obtained are not in accord with those of Salisbury (1927), who found that in the flora of British woodlands, stomatal frequency increased with the height of the species. It would appear, therefore, that although the leaf has a great potentiality to form more or less stomata according to the degree of humidity, stomatal frequency is in the first instance a specific character, a conclusion which has already been reached by Wood (1934) in his study of Australian plants.

The extent of variation in stomatal frequency shown by a particular species under different climatic conditions may well be connected with the system of venation of the leaf. The leaves of *Mimusops*, for example, with their close parallel veins, only show an increase in stomatal frequency of about 10% under dry conditions, while all the other species with reticulate or more widely spaced secondary veins show a much bigger increase ranging from 20 to 84%.

The probable effect of this type of venation on leaf form and its efficiency as an irrigating system has already been discussed above.

The increase in stomatal frequency as drier conditions prevail is accompanied by a reduction in area of the stomatal apparatus (Table II, cols. 7 and 8) but, whereas the mean increase in frequency for the nine species is 1.41, the mean decrease in area is only 1.12. It is also found that a considerable variation in stomatal area occurs from species to species, while the extent of variation induced by the environment is also extremely variable (Table II, col. 7).

The relations between frequency of stomata, area of stomata, and size of leaf are shown graphically in Fig. 3, in which the leaf area, together with the proportion of the leaf covered by stomata and epidermal cells, is indicated for each species. This diagram clearly shows that in spite of the smaller area of the stomata under dry conditions the relative area covered by the stomata is greater in the lowlands. This fact is further illustrated in Table II, col. 9, in which the percentage area of leaf covered by stomata is given. It will be seen that, with one exception, the percentage of leaf area covered by stomata is greater under dry conditions.

With regard to the frequency and size of epidermal cells it is also found that, in the lowlands, the number of epidermal cells per unit area increases (with the exception of *Doratoxylon*) while their size diminishes (Table II, col. 14). It will be noticed, however, that the increase in frequency of the epidermal cells is much less than that of the stomata. In the lowlands, for example, the average ratio between stomata and epidermal cells is one to eight, whereas, in the uplands the ratio becomes one to eleven. On the other hand, the relative decrease in area experienced by epidermal cells and stomata under dry conditions is very nearly the same (Table II, cols. 8 and 13). It will also be seen that the variation from species to species in epidermal cells both in area and number is much less than the specific variation of similar factors in stomata.

The stomatal indices of the various species (Table II, col. 14) as determined by Salisbury's formula offer some points of interest. The stomatal index is always higher under dry conditions, averaging 8.9 in the lowlands and 6.7 in the uplands. This indicates the formation of a larger proportion of stomate mother cells and is not in accord with Salisbury's (1927) conclusion that increased stomatal frequency of plants growing in dry soil is due to differences in growth of epidermal cells, that is, to the spacing of the stomata. It is clear that since the size of epidermal cells is only slightly reduced under dry conditions, the increased frequency of stomata must be due to some extent to an increased formation of mother cells.

The lowland leaf, therefore, is not merely a reduced facsimile of the upland leaf with consequently more closely spaced stomata and epidermal cells giving a higher frequency per unit area, but a leaf in which the relative frequency has increased owing to the formation of more stomata.

The increased frequency will be necessary to cope with the higher rate of

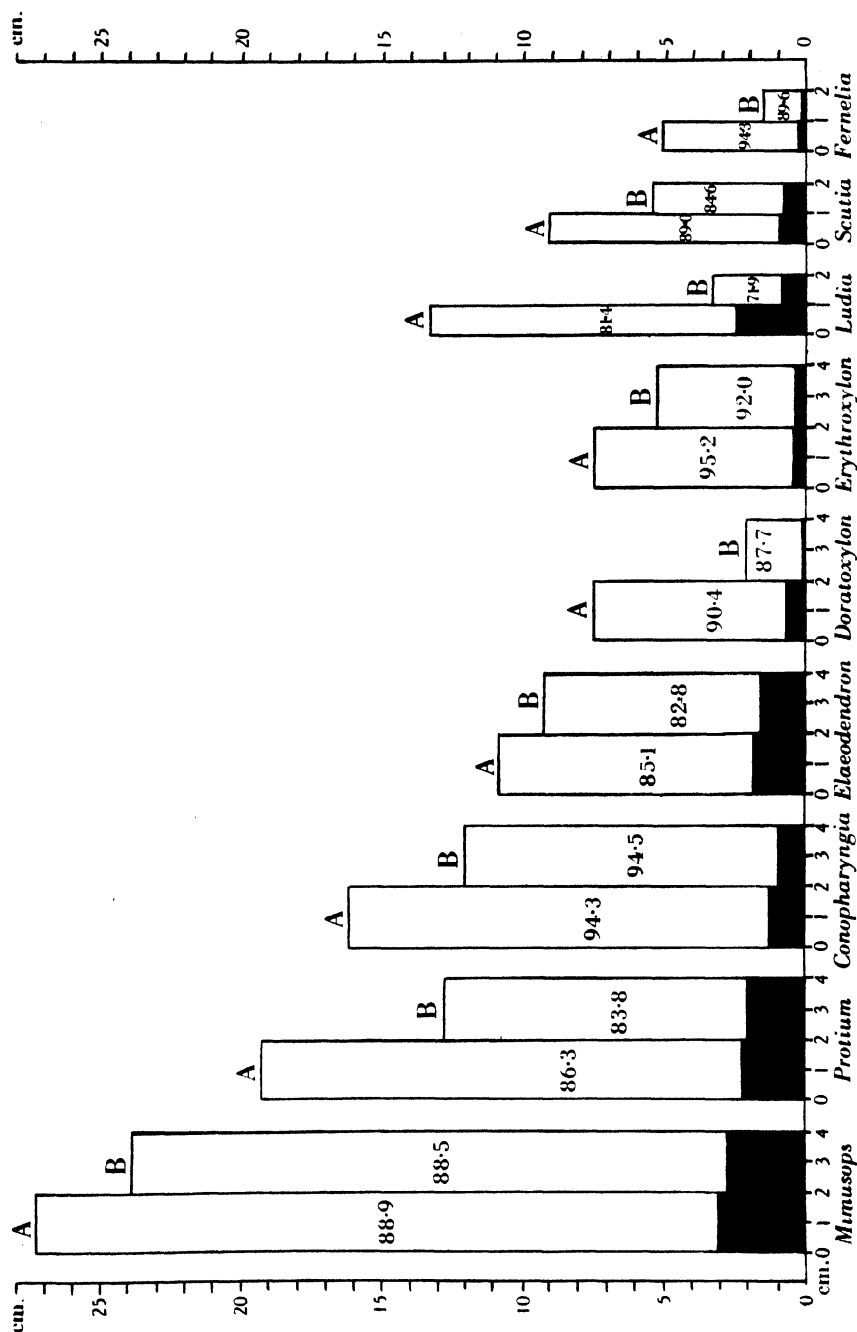


FIG. 3. Leaf area and stomatal area. The columns represent the mean leaf area of the species in the uplands A and the lowlands B. The mean area occupied by the stomata in each case is blacked in. The numbers give the percentage area of the leaf occupied by lower epidermal cells.

transpiration due to the steeper humidity gradient under dry conditions between the interior of the leaf and the atmosphere.

Further, the higher temperature and longer sunshine will result in an acceleration of plant metabolism with a consequent increase in the rate of gaseous exchange between the air and the leaf.

(c) *Note on variation*

It is not the purpose of this investigation to study individual variations and in any case the data obtained with the species *Fernelia* (Table III) in each locality is insufficient to enable any reliable conclusion to be drawn therefrom.

These figures are included because they seem to indicate that the amplitude of variation of which a species is capable may differ in the two localities.

It will be understood that the variation of any particular factor as revealed by a study of the species as a whole in the same habitat will be due to two causes, firstly the variation of the individuals among themselves yielding normal distribution curves, widely separated or close together, and secondly, variation within the individual yielding flat or steep normal distribution curves. The extent of these contributory causes of variation may be appraised by a study of the normal distribution curves and standard deviations.

Thus while variation in individuals of different habitats is always significant, an analysis of the figures in Table III shows that whereas variation in stomatal frequency and leaf length is not significant between lowland individuals, there may be a significant difference in both these factors between upland individuals.

The figures also tend to show that upland individuals are more variable within themselves (Fig. 4).

The comparative variation in two localities may also be gauged by the "coefficient of variability", an expression which yields a figure indicating the relative amount of variation in the particular locality and which is independent of the magnitude of the factor selected. In *Fernelia* the coefficient of variability is greater in the uplands both for leaf length and stomatal frequency.

It is not possible to say whether this is true for all the species investigated except in the case of stomatal frequency where the standard deviations have been calculated (Table II, col. 4). Here it is found that the coefficient of variability (or percentage standard deviation of the mean) is sometimes higher in the uplands and sometimes higher in the lowlands, the average figure for the nine species being 2.75 for the lowlands and 2.05 for the uplands. This capacity for variation under different climatic conditions probably has an important bearing on the species problem and deserves to be more fully investigated.

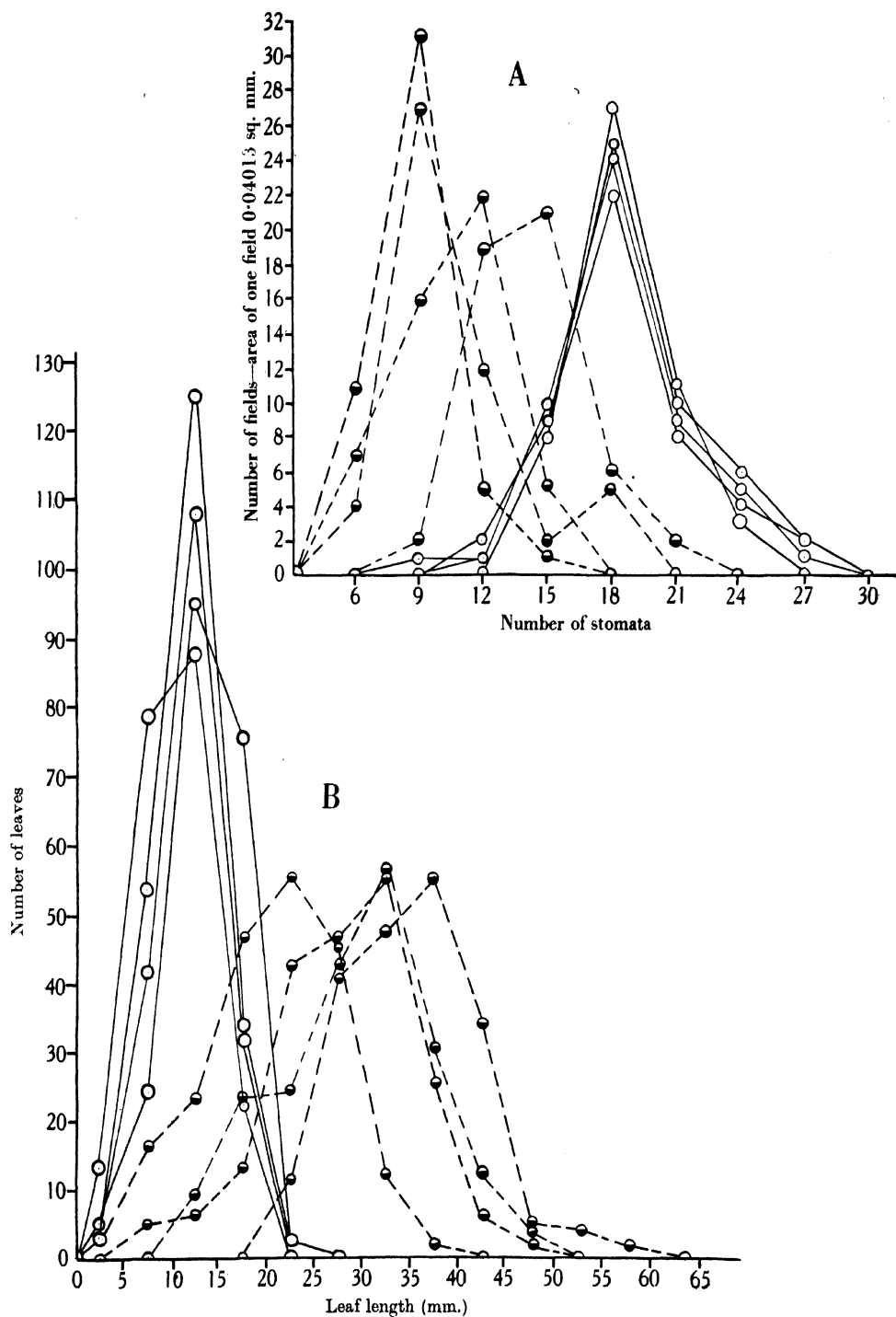


FIG. 4. Variation in stomatal frequency (A), and leaf length (B), of eight individuals of *Fernelia buxifolia* Lam., selected at random, four from the uplands (broken lines) and four from the lowlands (continuous lines).

V. SUMMARY

The variation in certain features of leaf morphology under dry and humid conditions has been investigated for nine indigenous species. The factors selected include leaf area and form, stomatal and epidermal cell frequency and area.

Meteorological data for the two localities are compared and the climate briefly described.

It is shown that dry conditions induce considerable changes in leaf form, and that these modifications are related to heterophylly, the xeromorphic significance of which is discussed.

Stomatal frequency is specific in character and a considerable increase is found under dry conditions, accompanied by a small decrease in area. The increase in frequency is partly due to an increase in the stomate mother cells.

The percentage area of leaf covered by stomata is found to be greater in the lowlands.

Lower epidermal cells show a smaller increase in frequency in the lowlands and the decrease in area is also small and comparable with that of the stomata.

The problem of variability in the individual and between individuals of the same species is discussed and the need for further research along these lines is indicated.

VI. ACKNOWLEDGEMENTS

Our thanks are due to Mr N. R. McCurdy, Director, Royal Alfred Observatory, Mauritius, for supplying us with much of the meteorological data used in Table I. Miss S. Ross Craig, Royal Botanic Gardens, Kew, has been kind enough to assist us in the preparation of Fig. 2.

REFERENCES

- BAKER, J. G. *Flora of Mauritius and the Seychelles*. London, 1877.
 BALFOUR, I. B. "The botany of Rodriguez." *Philos. Trans.* **168**, 1879.
 BRIGHT, D. M. E. "The effect of exposure on the structure of certain heath plants." *This JOURN.* **16**, 323, 1928.
 MAXIMOV, N. A. *The Plant in Relation to Water*. London, 1929.
 PARKIN, J. E. & PEARSON, H. A. W. "The botany of the Ceylon Patanas." *J. Linn. Soc. Lond.* **35**, 430, 1904.
 SALISBURY, E. J. "On the causes and ecological significance of stomatal frequency with special reference to woodland flora." *Philos. Trans. B*, **216**, 1927.
 VAUGHAN, R. E. & WIEHE, P. O. "Studies on the vegetation of Mauritius. I. A preliminary survey of the plant communities." *This JOURN.* **25**, 287, 1937.
 WOOD, J. G. "The physiology of xeromorphism in Australian plants." *This JOURN.* **22**, 69, 1934.
 YAPP, R. H. "*Spiraea Ulmaria* and its bearing on the problem of xeromorphy in marsh plants." *Ann. Bot., Lond.*, **26**, 815, 1912.

NOTE ON "THE PLANT COMMUNITIES OF MAURITIUS"
(This JOURN. **25**, 287, 1937)

We wish to take this opportunity of making a few emendations and additions.

Further information has come to light with regard to the introduction and subsequent spread of *Ligustrum Walkeri* and *Cordia interrupta*, two of the commonest naturalized species. Although it is true that *Cordia* was introduced in the manner stated in 1912, it had already arrived accidentally in the Island some years before, apparently in 1905, but did not spread. Species of *Ligustrum* have been known as ornamental plants for more than one hundred years but it was not until the beginning of this century, when it was planted for cover and utilized for firewood and charcoal, that the invasion of upland thickets by *Ligustrum Walkeri* began. Moreover, there is some doubt as to the botanical identity of this species with those introduced for horticultural purposes in the nineteenth century.

It is significant that both these species remained dormant and restricted in range for some years, awaiting a suitable means of distribution, and there can be little doubt that their ultimate rapid dispersal was due to birds, notably the Bul Bul (*Pycnonotus* sp.), introduced in 1891.

The creeper from Round Island reported as *Ipomoea pescaprae* Roth. (p. 333, line 31) is *Tylophora* sp., a native species.

For "south-eastern plateau" on p. 304, line 1 and p. 309, line 3, read "south-western plateau".

With regard to the distribution of *Rhizophora*, a small stand of mangroves occurs in a creek near Roche Bois, 2 miles north of Port Louis.

OBSERVATIONS ON TROPICAL AFRICAN GRASSLANDS

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(With Plates VII-XXIV, two Maps and five Figures in the Text)

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1. INTRODUCTION

THE writer became interested in grasslands and their causes when investigating the origins of the plagues of the red locust (*Nomadacris septemfasciata* Serv.). This insect, as well as its relative, the African migratory locust (*Locusta migratoria migratorioides* Rch. & Frm.), was found to be confined, when not travelling in swarms, to open grasslands, but not to any one form (10, 11). The distribution and nature of these grasslands therefore became a matter of practical importance as well as of theoretical interest.

In the following pages "forest" means dense, closed and more or less evergreen rain or fringing forest or related dense bush. In default of a better word "savannah" is used in its widest sense to cover all forms from open bush to woodland with a complete but light canopy of foliage, with grasses predominant in the undergrowth (unlike forest), and without dense understories of other herbs or bushes. It may be evergreen or deciduous.

The subject and the area involved are so large, that the limitations of this communication must first be mentioned. The writer is not a botanist and

approaches the subject as an amateur. Life in the bush has prevented search through the literature. Most of the suggestions made are due to personal observations, leavened by such remarks and writings of others as have come in the writer's way. The writer has been lucky in having been able to cover much ground during his eight and a half years in Africa, by foot, camel, canoe, car, train, steamer and air. Yet he still has no personal knowledge of West Africa, the forested Congo basin or the eastern corner of the continent. His travels include three years' residence in the central Sudan and two at Lake Rukwa in south-western Tanganyika, the transit of the whole length of the continent from the Cape to Cairo, extensive tours in the Sudan, Tanganyika and Northern Rhodesia, short tours in Uganda, Nyasaland and Southern Rhodesia, and glimpses, when passing through, of parts of the Belgian Congo, Kenya, Portuguese East Africa and the Union of South Africa.

It has not been possible to study the structure of the grasslands themselves. The matter considered has been the causes of the absence of trees, for in tropical Africa all land devoid of trees is grassland, unless it is permanent swamp, bare rock, salt pan or desert, or is cultivated or built on by man.

It is a difficult matter to fit grasslands into a general classification or map of the vegetation of the continent. In their very varied forms they cut across all zones of altitude, climate and vegetation. Although abundant enough, they are mostly too small in extent to be shown on any ordinary map. The new Beit Air Map of Northern Rhodesia (1) is an exception, for the importance as landing grounds of open ground in a wooded land has led to the intricate system of grasslands being mapped in all its details (Maps 1, 2). Schantz & Marbut (18) in their pioneer survey of the whole continent showed some of the largest open areas under the titles of Mountain Grassland and Swamp Grass, but had naturally to neglect all smaller areas on such a small scale map. Similarly, Henkel (5) could only map the largest areas in Southern Rhodesia, and could not show the large areas of plateau where trees are only dotted sparsely through the grass. Trapnell & Clothier (20), dealing with North-Western Rhodesia, map and describe the extensive alluvial and watershed grasslands under separate heads. The abundant smaller valley grasslands are not shown on their map, but the types of grassland associated with each woodland type are described with the respective woodlands. This is probably the best solution of the problem of how to fit the grasslands into a general vegetation classification of the continent; the grasslands themselves should be omitted from the primary classification, but for each zone based on the tree type the associated types of grassland should be described.

The writer first learnt to look with special interest on open grasslands in Northern Rhodesia. On the plateau of this country there is an extraordinary network of open grassy "dambos" or "vleis" following the streams, leaving the rest of the country entirely wooded. The regularity and the sharp edges of these dambos are especially striking when viewed from the air (Maps, 1, 2),



MAP. 1. Photograph of part of the Beit Air Map of Northern Rhodesia, showing typical plateau dambo country sloping down to the flood plains of the Lufunga Swamp. Open grassland is shown light, and woodland and bush are shaded, lightly below and darkly above the 4000 ft. contour.

when they are seen to form a perfect herring-bone pattern over the whole country. Wherever a stream cuts down into a valley with well-drained sides, the woodland comes down to the water's edge. Wherever the valley bottom becomes broad and flat, the dambo extends out sideways. During the rains the dambos are more or less flooded or waterlogged, while the woodland is well drained.



MAP. 2. Another section of the Beit Air Map, showing dambos and watershed grasslands along the crest of the Batoka Plateau.

Such a close correlation between seasonal waterlogging or flooding and absence of trees naturally led to the query whether other grasslands in other regions were due to the same cause. The presence of great seasonally swampy grasslands fringing the flatter shores of the larger rivers and lakes supported this view. The following pages examine the question further.

2. DISTRIBUTION OF OPEN GRASSLANDS

The distribution of the grasslands will now be given country by country for the southern and eastern half of Africa, where the writer has travelled, or which he has been able to visualize adequately from the remarks or writings of others. It has not been possible to include West Africa, but it may be expected that the open grasslands there are distributed according to the same rules as in the rest of the continent.

South Africa (14). Most of the northern part of the great central plateau is covered by the High Veld grassland. Southwards and westwards, as the rainfall decreases and approaches the mixed rainfall area transitional to the winter rainfall region of the South-Western Cape, the grassland merges into the Karroo, by replacement of the grasses by tiny undershrubs. In places, however, there is local desert grassland with scattered bushes. Westwards and

northwards there is mostly thorn and other bush country of the fringe of the Kalahari, the Bush Veld and the Limpopo valley. To the south-east the grassland rises to the mountainous rim of the plateau and descends the slopes towards the coast, where bush and forest appear. Patchy grassland extends to the coast itself, but extensive open country is confined to the inland regions.

South-West Africa (14). The country is covered largely with scrubby bush, becoming richer to the north, and giving way in the south to the floristically rich but far from luxuriant Karroo and Cape forms of vegetation. The coastal fringe is desert. Apart from local areas of open country with grasses of desert types, open grassland is almost confined to the neighbourhood of the great Etosha Pan in the north. To the north of the Pan there is much open grassland and grass and palm country flooded by the Cariango River, which drains into the Pan from Angola.

Bechuanaland is almost entirely occupied by the lightly wooded and bush country of the waterless Kalahari "Desert" (14). Although smaller open pans and vleis do occur further south, the only important open grasslands are the remarkable series of hollows occupied by the Okavango Delta, Lake Ngami, the Mababe Depression, the Makarikari Pan, and the swamps of the Linyanti or Chobe connecting with the Zambezi, which are actually in the Caprivi Strip of South-West Africa. These are described, mapped and photographed in the Report of the Kalahari Reconnaissance (6).

Portuguese East Africa is composed of tropical and subtropical woodland and bush country, with a few rain forests, and with open grasslands in certain of the flood plains of the rivers near the coast.

Southern Rhodesia is a plateau bounded by the great wooded valleys of the Limpopo and the Zambezi to the south and north respectively. The plateau itself is also largely covered with bush and woodland, but the moister part to the north-east, Mashonaland, is largely open grass, with trees confined to rocky hills, especially in the highest parts (Phot. 16). The still moister highlands of the Eastern Border country, overlooking the Portuguese lowlands, are also largely open grass with patchy bush, dotted trees and a few small rain forests (Photos. 29, 30, 31, 32). Descending from the open uplands of Southern Rhodesia one at once enters bush and wooded country where open ground is confined to the vlei or dambo drainage lines and valleys. On the steeper slopes and low country even these are wooded.

Nyasaland is a varied country having much in common with Rhodesia and with Portuguese East Africa. In the lowlands flood plain grasslands occur in the Lower Shire valley at Port Herald and above Chiromo (Phot. 5), locally in flat parts of the shores of Lake Nyasa, and in the depression in which are the Lakes Shirwa (Chilwa) and Chiuta, the latter of which stretches into Portuguese East Africa. Dambos of the same kind as those of Rhodesia occupy gentle valleys in wooded country at all elevations (Phot. 10). Hilly open grasslands at high elevations, continuing the line of the Drakensberg and Southern Rhodesia

Eastern Border ranges, occur on the summit plateaux of Mlanje and Zomba Mountains (Phot. 34) in the south, and on the highest parts of the plateau west of Lake Nyasa in the north.

Northern Rhodesia is devoid of rain forest but is almost entirely covered with woodland and bush. On the Batoka Plateau in the south there are some areas resembling the Mashonaland grasslands. These are classed by Trapnell & Clothier (20) with some other isolated patches as Watershed Grasslands, of which much larger expanses exist on sandy plains above the western side of the Upper Zambezi and stretch far into Angola. Other open grasslands of any extent are confined to flood plains and their fringes. The chief ones are the Barotse Plain and Simaraha Flats of the Zambezi, the Busanga and Lukanga Swamps and the Kafue Flats of the Kafue in North-Western Rhodesia and the fringing plains of Lake Bangweolo and certain valleys of the Mweru-Tanganyika Lowlands in North-East Rhodesia (Phot. 6). The whole of the plateau and much of the lowland country is covered with the network of open dambos along the valleys already described (Photos. 7, 9, 11, 12, 13). In a few of the highest parts of the plateau, chiefly along the northern borders, the grasslands spread up the valley sides from the true dambo bottoms and show some approach to plateau or watershed type.

Angola is little known to me, but it is known that the country is mainly wooded. Away from the arid coastal lowlands, the interior plateau, to a large extent, has a network of valley dambos like that of Rhodesia. Open sandy plains, with a scarcity of water in the dry season, occupy the plateaux in the south-east as just mentioned, Bihé in the centre and Lunda in the north-east (21). These plains are seamed by rivers running in deep wooded valleys.

The Belgian Congo. The woodlands of Northern Rhodesia stretch northwards into the Congo with increased tropical luxuriance as the rainfall increases. The southern part resembles the adjoining parts of Northern Rhodesia, with dambos running through woodland country, and these are said to continue far northwards through vegetation of increasing luxuriance. There are extensive open grass plains in the valley of the Lualaba River, with its string of lakes and swamps, and there is a strip of open flood plain on the west bank of the Luapula, which is said to extend north to Lake Mweru. There are said to be large plateaux of grazing country, especially in the Lomami area of Katanga.

The following notes on the northern half of the Congo are taken from Lebrun (7) and Robyns (16). In the forest region itself the grasslands are restricted to two types, apart from the swamp grasses fringing the rivers. In the low, swampy, western part of the basin Robyns describes, under the native name of "esobe", occasional small clearings near the river. In the north of the country small areas of lateritic platforms inside and outside the forest are occupied by open grass dominated by *Ctenium Newtonii* Hack. or *C. elegans* Kth., with dotted mixed bushes of forest and savannah affinities in pockets of deeper soil. Round the fringes of the equatorial forest the following grasslands

lie. Lowland grass plains and areas with only scattered trees alternate with forests and denser savannah in the river valleys round the south-western edge of the forest and even form clearings in the forest itself. Others exist along the Lomami and Lualaba rivers and in the valleys of the upper Uele basin. In the western branch of the Rift Valley they lie in the flatter parts of the Ruzizi, Rutshuru and Semliki valleys and round Lakes Edward and Albert. In the north-east of the Congo there are considerable areas of sparse savannah parkland, grading at the higher altitudes into open grasslands. The drier north-eastern grasslands are characterized by *Themeda*. Further south, above Lakes Edward, Kivu and the north end of Tanganyika, bracken (*Pteridium*) is often abundant, and the grassland is certainly secondary, often forming a belt between the main equatorial forest and the mountain forests. Other secondary grasslands which have been formed by destruction of the forest are those of *Imperata cylindrica* (L.) Beauv. var. *Thunbergii* Hack., of *Panicum maximum* Jacq. and of *Pennisetum purpureum* Schum. (elephant grass). *Imperata* is widespread in Ubangi district, and considerable areas also exist near Amadi and other parts of the upper Uele and near Rutshuru in the Rift Valley. The *Pennisetum* chiefly occupies heavier soils in the wetter mountain areas of the east, as well as in the main forest basin, but this giant species can hardly be said to form grassland in the ordinary sense, any more than can the mountain bamboo forests. The alpine meadows of Ruwenzori and the Kivu mountains are grasslands of small extent but great interest.

Ruanda-Urundi, formerly the north-western part of German East Africa, is a high, broken country, largely composed of bare, grassy hills. Flat grassy plains occur along the Kagera River on the Tanganyika boundary.

Tanganyika Territory is a country of wooded and bushed plains and plateaux, like most of tropical Africa. The numerous rifts and step faults connected with the Great Rift Valley system have broken many of the drainage lines and given rise to a number of grassland areas. Starting in the west, one finds the north-western Highlands forming a continuation of the grassy hills of Ruanda-Urundi, while the higher parts of the Ufipa Plateau in the south-western corner, between Lakes Tanganyika and Rukwa, are largely open grassland (Photos. 14, 15). In the western arm of the Rift Valley system the waters of Lakes Tanganyika and Nyasa lap the steep shores, but Rukwa only partly fills its flat valley floor and is fringed with a grassy flood plain, especially on its northern and western sides (Photos. 1, 2). The great plateau of the centre and west of the country bears numerous "mbugas", corresponding to the dambos and vleis of farther south, in hollows liable to flooding and water-logging. Amongst the largest of such areas are the plains of the middle Malagarasi and the great Usinge Swamps (Phot. 8) draining into them from the east, the flood plains of the Ugalla River, large mbugas south of Lake Victoria, and the Wembere Steppe. The last lies in a trough which is one of the southern extremities of the eastern branch of the Rift Valley, in which grassy

plains occupy the depressions in many parts, especially near the lakes and round the pan which receives the waters of the Bubu River. On the highlands overlooking the branches of the eastern Rift Valley there are some rolling upland grasslands, especially on the Iramba Plateau and the Mbulu Highlands. The famous Ngorongoro Crater is also mainly open grass. Further south the faulted troughs of the Great Ruaha, Kilombero and Mkata Rivers contain grassy flood plains. The largest expanse of grassland in the country occupies the great triangle of high, broken country extending from Mbozi and the eastern side of Lake Nyasa up to Iringa (Phot. 33), with outliers on mountain masses still further north-east. Some of the rivers of the coastal lowlands run through grassy, alluvial flats. The extreme north-west corner of the country adjoining Uganda has many swampy and grassy valleys running into Lake Victoria. In the north-east of the Territory the dry plains of the Masai Steppe are mainly covered with thorn bush but contain broad mbugas in the hollows, while the Serengeti Plains, on the opposite side of the Rift Valley, are also arid thorn country with much open grass.

Kenya. Much of the coastal lowlands is covered with dense scrub, but the Kenya Highlands, from the Tanganyika border northwards, are largely open country. Broken country at moderate elevations and in dry regions is mostly clothed with bush of one kind or another. The higher and wetter mountains bear rain forest. Most of the less broken ground in the Highlands, even in the Rift Valley, is open grassland. In the wetter parts the grassland also grows at high elevations alternating with forest. On the highest mountains of East Africa a partly grassy moorland occupies a zone above the forest belt. The rest of Kenya towards the north and north-east consists of immense plains covered with arid and semi-desert forms of vegetation, in which sometimes thorn bushes and sometimes open grasslands predominate. In this region the Lorian Swamp is surrounded by open grassland and itself dries up frequently.

Uganda. In the countries south of Uganda the sharpest changes in climate from place to place are due to changes in altitude. Uganda differs in having a great variety of climate and vegetation within its small area, without a corresponding variety of scenery. The main continental climatic belts themselves are telescoped together here. The centre of the country near Lake Victoria is the remains of a plateau, much broken up by small valleys containing papyrus swamps, which are sometimes fringed by small boggy stretches of grass. The hills are largely cultivated and to a great extent covered with the giant elephant grass (*Pennisetum purpureum* Schum.), much of which is secondary to rain forest, of which remnants exist in parts (Phot. 35). As Lake Victoria is left further behind in any direction, the valleys flatten out and the climate becomes drier, so that open grassy valley bottoms appear. To the north and north-east the country becomes arid, so that the mbuga valleys disappear again, but the general bush covering of the country becomes sparser, leaving stretches devoid of trees (Photos. 23-26). This type of country merges into the similar parts of

Kenya, Abyssinia and the Sudan adjoining. To the west both the country and the rainfall are higher than in the north and east, with the result that open grasslands, or country only dotted with trees, or with ant-hills covered with bushes, appear on the flat topped hills as well as in the valleys (Photos. 21, 27, 28). On the edge of the western Rift Valley the rainfall increases again, and rain forest and scrub secondary to forest oust the grasslands from most of the country. South of Fort Portal there is an area where the whole face of the country is a solid mass of elephant grass with hardly a tree anywhere, perhaps secondary to forest, but this terrible jungle can hardly be called grassland. The Rift Valley itself bears a curious patchwork of arid thorn bush (Phot. 18) and closed forest, with extensive grass plains (Photos. 17, 19, 20) round Lakes Edward, George and Albert and in the Semliki valley. The valley of the Albert Nile contains bush and woodland, but parts of the highlands overlooking it bear fairly open grassland.

Somaliland and Eritrea are not known to the writer personally and can only be briefly mentioned. The coastal lowlands are hot semi-desert with thorn scrub and doubtless such areas of open desert grass as occur with such country elsewhere. Parts of the interior are high, cool and less dry and approach the open country of Abyssinia in character.

Abyssinia. The fringes of the country are arid and thorny, like the surrounding countries. Grassy plains of semi-desert nature probably occur in the Rift Valley and elsewhere, especially near the lakes. Much of the mountainous centre of the country is open grassland, other parts being bushed, forested or heavily cultivated.

The Anglo-Egyptian Sudan. The Imatong Mountains (3), on the extreme southern edge of the country, bear types of grassland commoner further south in regions of higher rainfall. The swamps of the White Nile are fringed by enormous grassy plains of heavy soil, liable to flooding in the rainy season (Phot. 3). The whole of the rest of the country is an immense arid plain stretching north into the Nubian Desert, relieved only by the Nile and its few tributaries, and by the Red Sea range and other scattered mountains and groups of hills. South of the desert the country is covered with thorny scrub, becoming woodland up the Blue Nile and locally elsewhere in the south. In many parts the bushes have been cleared off for firewood or cultivation, leaving artificial grassland or bare ground. Here and there patches seem to be naturally devoid of bushes. In the south, perennial grasslands occupy these spaces; further north, some of them bear only a scanty growth of annual grasses. In the better watered country of the extreme south-west, near the Nile-Congo Divide, there are some valley grasslands not unlike the Rhodesian "dambos".

3. TYPES OF GRASSLANDS

The rough survey given above shows that grasslands are widespread in the Ethiopian region and occur at all altitudes. The most extensive grasslands are those of the rolling uplands in Abyssinia, in the equatorial belt of East Africa and in South Africa. The flood plains of the great rivers and lakes bear large stretches of open grass also. Grasslands, individually of small extent but large in the aggregate, are formed along the drainage systems of the plateaux and plains of moderate rainfall. Even the semi-desert regions have some open grass areas, though they are less clearly defined than elsewhere. The grasslands will now be described under five heads, arranged for convenience according to climate and physiography.

A. *Flood plains* (Phots. 1-8, 15, 21; Map 1; Fig. 1 A). Alluvial plains liable to flooding by rivers and lakes are nearly treeless. Some palms (Phot. 8) and acacias (Phots. 4, 8) may grow in parts. In places reached only by occasional floods there may be more numerous trees and bushes, especially species of *Hyphaene*, *Borassus*, *Acacia*, *Combretum*, *Bauhinia*, *Ficus* and *Kigelia*, but they are only dotted about in the grass. The grasses are too varied to specify, but are commonly rank. Admixture of other herbs, other than sedges, is usually small, increasing as permanent swamp conditions are approached. The soil is usually a heavy clay, often dark in colour and liable to crack when dry. Where the flood water is brackish, the grass is finer in texture and composed of fewer species specially adapted to such conditions (Phots. 1, 2, 6). The soil is also of a different texture, being often light in colour and not cracking much when drying. In a normal cycle of erosion, flooding is caused only when rivers have reached their base level. Accordingly, some flood plains of this sort are found on the lower courses of the few rivers which cross the narrow coastal plains of Africa. The continental drainage lines have, however, been greatly modified in Tertiary times by warping and faulting, especially by the Great Rift Valley and its branches. By these earth movements lakes and dischargeless hollows have been formed, some rivers have been dammed back, others have been diverted to new courses, and a few have even been made to run backwards. It is therefore in the troughs and hollows of the Rift Valley system that most of these flood plains must be sought. A few, like the Etosha Pan, the Lorian Swamp, the White Nile sudd and the swamps of the middle Niger, are due to warping unconnected with the Rift, or to delta formation in a river running towards a desert. They are naturally most numerous where the rainfall is moderate or high. A markedly seasonal rainfall will tend to cause bigger flood plains than a well distributed one, but in Africa this effect is masked by the structures of the country.

B. *Small valley grasslands* (dambos, vleis) (Phots. 9-15, 17, 19; Maps 1, 2; Fig. 1 B). These are best developed in regions of moderate rainfall and temperature, such as the plateaux of the southern tropics. They differ from the flood

plains in being partly sloping and not entirely covered by flood water. They may occur in the sides and bottom of a gentle valley, or may be situated on a gently sloping hillside. The centres may carry actual surface flood water

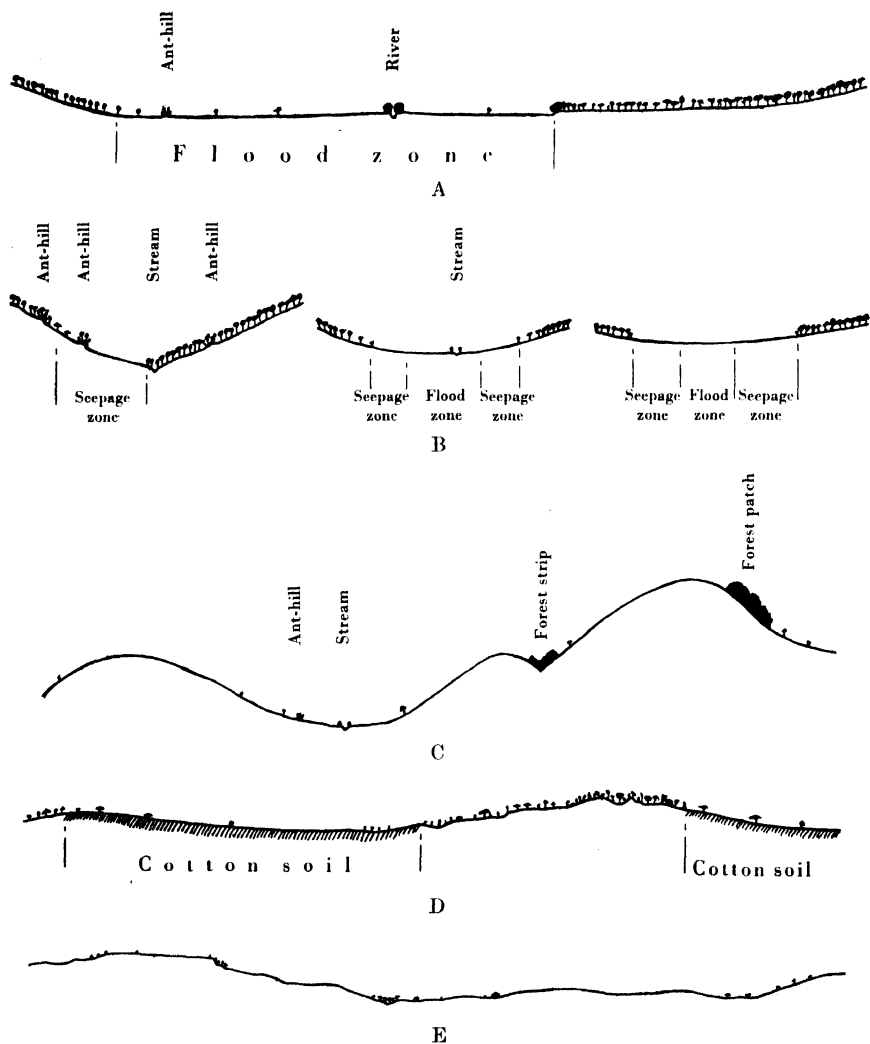


FIG. 1. Diagrammatic profiles of grassland types. A. Flood plain grassland. B. Small valley grasslands. C. Upland grassland. D. Cotton soil grassland of arid country. E. Desert grassland.

(Phot. 15), but the sloping side parts owe their existence to waterlogging by seepage water during the whole or part of the year. This is the reason for their scarcity in regions of low rainfall and high evaporation. Some have a seasonal or perennial stream in the middle (Phot. 12), others form grassy troughs half full of running water during the rainy season (Phot. 15). The grass is usually

fairly fine (Photos. 12, 14, 15), though it may contain very tall kinds like *Hyparrhenia* (Photos. 9, 10, 11, 17). In dambos damp through much of the year there is usually a rich variety of sedges and flowering plants with the grasses, many of them flowering in the dry season. The soils are variable. In drier climates, at lower altitudes and in regions of more basic rocks, there may be dark, cracking clays with lime nodules. In wetter climates, at higher altitudes and on more acid rocks there are often white or yellow clays and sands, with a tendency towards the formation of peat and of ironstone pan and probably of an acid reaction. Sometimes small dambos owe their origin to the presence of an impervious ironstone pan a little below the surface. Where, however, the secondary ironstone actually outcrops, so that there is no surface soil to hold the water, cracks in the rock usually support such trees as *Pterocarpus angolensis* DC., *Hymenocardia mollis* Pax and *H. acida* Tul. Lebrun (7) and Robyns (16) describe similar patches of short grassland on laterite pans, dominated by *Ctenium elegans* Kth. and *C. Newtonii* Hack., near and even inside the north and north-west parts of the Congo rain forest. In these shallowness of the soil prevents the growth of forest, while seasonal waterlogging excludes the savannah trees. Dambos are sharply defined at the edges when traversing fairly dense bush, such as *Brachystegia* woodland (Phot. 11). When surrounded by Combretaceous or Transitional (20) Bush the limits are less clear (Phot. 10). In *Acacia* country there are often no clear edges at all, as certain *Acacias* can grow in dambo conditions (Photos. 17, 19). In grassy upland regions there may be no clear line between the part of the valley liable to waterlogging and the dry hillside above it, both being equally treeless (Photos. 14, 15, 16, 34).

C. *Upland grasslands* (including mountain, plateau and watershed grasslands) (Photos. 16, 21, 27-34; Map 2; Fig. 1 C). These differ from the flood plains and small valley grasslands in not being confined to the drainage lines, but in stretching over hills and valleys, sometimes on steep slopes. They exist only in subtropical and temperate climates and are therefore confined to high altitudes in the tropics, only approaching sea level in South Africa. They are often associated with rain forest (Photos. 32, 34). In the grasslands there are often dotted evergreen trees and bushes of upland savannah affinities, such as *Parinarium*, *Brachystegia*, *Protea*, *Dombeya*, certain species of *Acacia*, *Faurea*, *Rhus*, *Gymnosporia*, *Cussonia*, *Erythrina* and many others. There is usually no sharp line between open grassland and areas of savannah woodland or bush, such areas of dotted trees and bushes forming a transition (Photos. 21, 28). In other parts there are little clumps of trees and bushes of forest affinities. These are often grouped round an ant-hill or a larger tree. In some particularly interesting areas these elements of the savannah and the forest floras grow side by side in the grassland (Phot. 33). The grass itself is usually fairly short (Phot. 34), in accordance with the climate, though tall species may grow in more sheltered and damper valleys, on disturbed ground, or near forest patches in places where this type of grassland grows at lower elevations, as in parts of

the eastern border of Southern Rhodesia (Phot. 32). Of the numerous grasses which occur, *Themeda triandra* Forsk. is the most characteristic and widespread. Amongst the grasses there is a wealth of flowering herbs, many of them geophytes, growing up and flowering in the latter part of the dry season and early part of the rains, before the grass overpowers them (Phot. 33). Of tougher plants *Smilax*, *Asparagus* and bracken (*Pteridium*) are common in the grass. The two previous types of grassland, the small valley and flood plain types, occupy the bottoms of some of the wider valleys in this type (Phot. 21). The types grade into one another so gradually, that in classifying or mapping an area of upland grassland it would be difficult to separate the other types except in a detailed survey of a small area.

D. *Cotton soil mbugas and pans of arid country* (Photos. 22-6, Fig. 1 D). It has already been mentioned that valley grasslands in regions of low rainfall and high evaporation usually have dark, heavy, clay soils, which crack badly in the dry season. In the hot, dry countries, which are mainly covered with species of *Acacia* and other thorny trees and bushes like *Zizyphus*, *Balanites* and *Dichrostachys*, most gentle valleys and even flat plains are covered with these so-called "cotton soils". Large plains of this type have often been described as alluvial. Although this may be true in part, many of the smaller areas can only have been formed by accumulation of colluvial soil by surface washing through long ages. The characteristics of such soils are less due to the topography than to the climate, which exposes the soil to great extremes of temperature, wetness or dryness, and which prevents such thorough removal of soluble salts as in wetter countries. Parts of these cotton soil bottoms and plains are often open grassland. In the less arid regions the grasslands are like dry forms of the small valley grasslands already described (Phot. 25). In drier countries the grasslands follow the drainage lines less and less (Photos. 23, 24). This is partly because the decreased rainfall is no longer enough to cause waterlogging of the valley soils, but runs quickly off in sandy "khors" or "dongas", which are dry except just after rain. Partly it is due to the capacity of certain species of *Acacia* and other bushes for colonizing heavy soils with bad water conditions. Some of the Gall Acacias, such as *A. formicarum* Harms, *A. drepanolobium* Harms, and *A. Seyal* Del. var. *fistula* Oliv., as well as the ungalled typical *A. Seyal*, grow commonly on cotton soil mbugas, which without them would be open grasslands (Phot. 22). Although such grasslands are less closely connected with drainage lines than in moister and cooler climates, yet their causes are largely the same. Dry cotton soils will absorb much water in breaking down their hard clods, without leaving any available for plants. This is shown in the early rains, when seedlings and dormant roots quickly sprout on sandy and gravelly soil, but on heavy clays nothing appears till much rain has fallen. On the other hand, heavy rain soon puddles the surface and lies about till it evaporates or drains slowly off the flat ground. Conditions are therefore so bad for plant growth, that trees often fail to colonize such

areas, though the hardy grass family supplies some species which can exist and form grassland. Cotton soil grasses are usually of a coarse growth compared with the species growing on adjacent lighter soils. Associated herbs are usually sparse, but include coarse annuals which grow up with the grass.

E. *Desert grasslands* (Fig. 1 E). As the extremes of drought are approached, plant life dies out. On the fringes of the deserts water is so scarce that waterlogged, treeless, grassy hollows can no longer exist. On the contrary, it is now rather the drainage hollows that support the bushes, while perennial grasses can still struggle on in less favoured spots. Elsewhere bushes may be found stretching further into the desert than the grasses, which are either almost absent or only present as annuals, which can hardly be considered as forming grassland. Desert grasslands, being open, usually contain a good variety of herbs and undershrubs. In the "gizu" regions of the Sudan (9, 12), grasslands on the fringe of the desert give way to a scattered growth of low herbs. The factors determining whether grasses, bushes or low herbs shall be dominant are not clear and may vary from place to place, but they are doubtless mainly connected with water supply. In brackish soils along the coasts and in brak pans of East and South-Western Africa special salt-loving herbs and undershrubs, particularly Chenopodiaceae, oust the grasses.

Although it is not desert, reference may here be made again to the transition between the subtropical grasslands and the temperate Karroo vegetations of South Africa. South Africa, is on the whole, a strikingly treeless country, the climate of the drier parts being evidently in some way unsuitable for trees. The grasses stretch south-westwards better than the trees, till they are met by the dwarf undershrub formation of the Karroo. In the transition areas the appearance of the vegetation varies from year to year. In a year of plentiful rain the country appears grassland, with a plentiful mixture of bushy Karroid plants. In dry seasons the latter dominate, and grasses are as scarce as they are in the middle of the Karroo in a normal season.

4. CAUSES OF GRASSLAND FORMATION OTHER THAN WATERLOGGING

It has been shown above how flood plain, valley and cotton soil grasslands are due to prevention of tree growth by waterlogging. It has also been shown that desert grasslands are due to absence of trees owing to lack of water, but it is not possible here to discuss the details of the distribution of open grassland in the desert fringes. There remain the problem of the origin of the rolling upland grasslands, and certain other factors that may prevent tree growth.

A. *The problem of the upland grasslands.* Most other kinds of grassland being caused by periodical excess of soil water, it is interesting first to see how far the more extensive upland grasslands can be due to the same cause.

In plateaux with low relief the rivers running over the edge are often fringed with valley dambos. Upstream, as the valleys widen and become shallow,

merging into the gentle undulations of the plateau, the grasslands also widen and join, till the flat summit of the tableland is all open grass. This gives the impression that the same poor drainage, which is confined to the gentle valleys on the sloping sides of the plateau, is more widespread on the flatter summit. This is the typical watershed grassland, an excellent example of which is the grasslands of Mashonaland in Southern Rhodesia (Phot. 16; Map 2; Figs. 2 A, 3 A).

Further evidence for waterlogging being the cause of the absence of trees is the wide distribution of ironstone pans, and of grasses like *Trichopteryx simplex* Nees, which indicate panned soils, in Mashonaland and other similar areas.

The distribution of the trees themselves again supports this view. Where steep and stony hills rise from such an open grassy plateau, they are nearly always wooded. This condition of wooded kopjes rising above gentle grassy slopes is strikingly shown in Mashonaland (Phot. 16), and may be seen also on the hill ranges of the Ufipa Plateau of Tanganyika (Phot. 14). Where rejuvenation of rivers has started active erosion along the valleys back into the grasslands, the grassland tongues do not stretch down the valleys, which are here too steep and well drained, but on the flat spurs between them (Figs. 2 B, 3 B). As an example may be given the Transvaal High Veld between Pretoria and Johannesburg. In the watershed grasslands on the Angola-Rhodesia border (20), and on the Lunda Plateau of Angola, (21) somewhat similar conditions exist, for the flat plains are traversed by steep-sided eroding valleys whose sides are clothed in bush or forest.

Again citing Southern Rhodesia, another piece of evidence exists north-west of Salisbury and is particularly well seen from the air (Fig. 4). Flying from the Northern Rhodesia plateau, with its herring-bone pattern of dambos set in a background of *Brachystegia* woodland, one crosses the rift valley of the Zambezi. The floor of this has too arid a climate, due as much to high evaporation as to low rainfall, to support dambos, while the form of the main rivers here prevents the formation of flood plains. The steep escarpments and the broken country to the south are too well drained to have dambos. The gentler slopes of the Southern Rhodesian plateau further on have the usual pattern of dambos along the valleys. This is brought to an abrupt end by a range of hills, the Mvukwe Hills, which are formed by an ancient intrusion, the Great Dyke of norite, which traverses the whole country. On the south-eastern or upper side of this range there is a belt of open grassland, sprinkled with *Parinarium* trees and with patches of *Brachystegia* on the better drained ground. Henkel (5) maps this as *Parinarium* country and describes it as being plentifully invaded by *Brachystegia*, but my observations in various countries indicate *Parinarium* as being a normal constituent of the upland forms of *Brachystegia* woodland, which is able to stand rather poorer drainage as well as a cooler and wetter climate than most species of *Brachystegia*. Beyond this open belt lies the normal plateau vegetation of

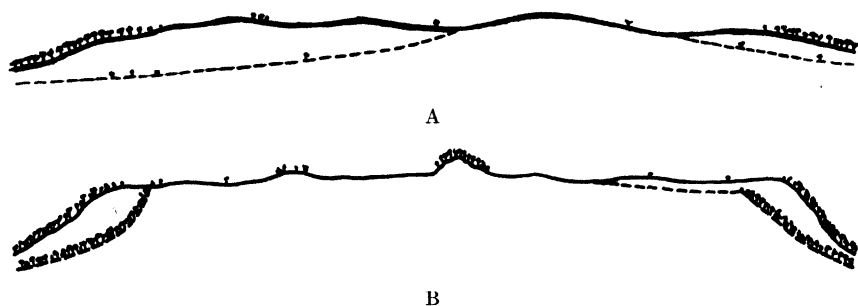


FIG. 2. Diagrammatic profiles of watershed grasslands. (Outlines of crests represented by full lines, of valleys by dotted lines.) A. Plateau drained by fairly mature valleys (cf. Fig. 3 A). B. Plateau drained by young eroding valleys (cf. Fig. 3 B).

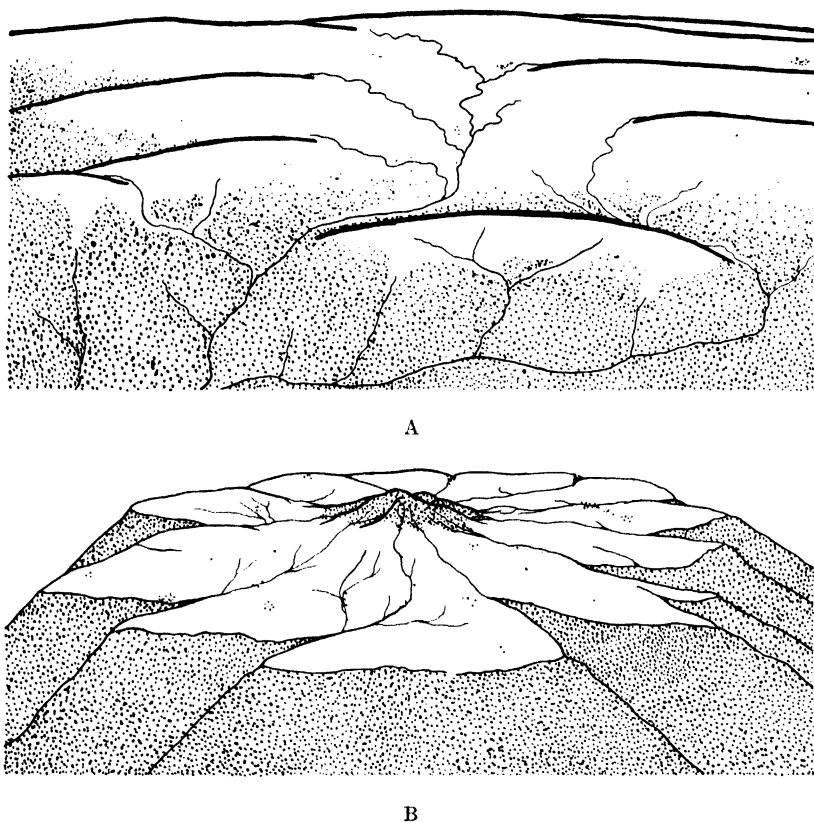


FIG. 3. Diagrammatic sketches of watershed grasslands. (Trees represented by dots, grassland undotted.) A. Plateau drained by fairly mature valleys (cf. Fig. 2 A), with tongues of open grassland running down the valleys. B. Plateau drained by young eroding valleys (cf. Fig. 2 B), with tongues of bush running up the valleys.

Mashonaland, largely open grass, with numerous patches of *Brachystegia* woodland on hills and elsewhere. It is clear that the Great Dyke acts as a sill, which holds up the drainage of that side of the plateau, causing more water-logging and consequently less wooding on its upper side than elsewhere.

The influence of climate as well as of topography in controlling the distribution of grassland is also shown in Southern Rhodesia. Although the plateau stretches right across Mashonaland and Matabeleland into the Kalahari Plain (5, 8) and the Matabeleland part is no better drained than Mashonaland, yet the grasslands are poorly developed in Matabeleland. This is because Matabeleland has less rain and higher temperatures than Mashonaland, so that the soil has less chance of becoming waterlogged.

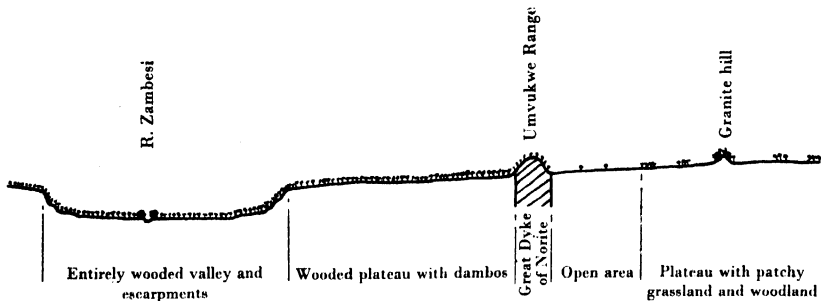


FIG. 4. Diagrammatic section from Zambezi valley to Mashonaland plateau.

This imposing array of evidence is opposed by a number of facts. Firstly, open grassland occurs on some hill slopes far too steep ever to become waterlogged. This is so particularly in mountainous regions of low temperatures and high rainfall, where the grasslands are associated with rain forest (Photos. 27, 29, 32, 34). Even this fact in a way supports the case for lack of drainage being the cause, for it has already been shown, that the greater is the amount of soil moisture, the more widespread are the open grasslands. In these cold, wet highlands, the grasslands extend even on to steep slopes. Also the soils of hillsides in such regions are more loamy and retentive of moisture than the stony soils usual on steep slopes at lower elevations. It may therefore be that the trees and bushes of the African savannah are unable to stand a soil which is well watered all through the year, even though it is never waterlogged.

Differences in rock may act in a similar way through the soil. On the Northern Rhodesia-Tanganyika frontier there is a striking change of vegetation. North-Eastern Rhodesia is mainly a plateau of 4000 to nearly 6000 ft. altitude, covered with *Brachystegia* woodland and bush and rich in dambos and clear running brooks. The north-eastern part of it is formed by the slightly tilted sandstone of the Palaeozoic Katanga System. Along the border there is granite in parts. Beyond this, in Tanganyika, the highlands are mainly composed of Basement Complex schists, while round Mbeya and Tukuyu there are Tertiary volcanic rocks. On the Tanganyika side of the border the woodland

and bush become much more restricted (Photos. 14, 15), and much of the country is open grassland, while many of the watercourses are strips of sedgy swamp. Although this change coincides with an increase in altitude and therefore a change of climate, it is tempting to believe that at least part of it is due to soil differences. The sandstones give rise to quick-draining sandy soils, suitable everywhere for bush, except where the water seeps out again in the dambos. The richer soils in Tanganyika drain less well and consequently bear more open grassland.

The influence of climate, acting through the soil, on vegetation on mountain slopes is clearly shown between Melsetter and Umtali in the eastern border of Southern Rhodesia. The road from Melsetter climbs up the mountainous valley of the east-flowing Msaaps River. This valley is open grass on red-loamy soil, with patches of stunted woodland of *Brachystegia* type (*B. Bragaei* Harms., *Isoberlinia globiflora* (Benth.) Hutch., and *Uapaca Kirkiana* Muell. Arg.) on some of the slopes, and lank evergreen scrub in moist gullies (Phot. 29). At Msaaps and Commik Neks the road climbs out at a height of 6000 ft. into the head of a west-running valley, whose steep slopes are mainly covered with shallow, poor-looking whitish and yellowish soil and with scrubby *Brachystegia*, *Philippia*, *Faurea* and *Protea* (Phot. 30). The gullies are still occupied by rich evergreen scrub, including the cypress, *Widdringtonia*. Going round the head of this valley, the road at Moodies' Nek crosses over into another east-running valley, where there is again much open grass on redder and richer-looking soil, but with *Brachystegia* bush still on the poorer patches. It is clear that the richer soils in this area favour open grassland, while the poorer ones favour *Brachystegia* and its associates. The soil differences between the valleys may be partly due to the rocks, for dolerite intrusions occur in parts of the Msaaps Valley, but mainly they seem to be due to climate. The eastward facing valleys look towards the coast, while the westward ones face the dry interior and probably receive less rain and mist. Other valleys along this watershed show the same thing. For instance, one trough cutting right across the crest is mainly open in its eastern half, which forms the east-running valley of the River Lusitu, while its western part, in which runs the River Tanganda, is entirely wooded (Fig. 5).

There is another fact which suggests that there are differences between the soils of grasslands and of woodland and bush country other than the water supply. In arid climates the genus *Acacia* dominates the vegetation. In regions of moderate rainfall such species of this group as occur are much more restricted. Though certain species occur elsewhere, the chief Acacias are confined to rich alluvial or the best colluvial soils. With them are associated such other species as *Bauhinia Thonningii* Schum., *Ficus Sycomorus* L., *Zizyphus jujuba* Lam., *Kigelia pinnata* DC., *Hyphaene* sp., *Borassus flabellifer* L. var. *aethiopum* Warb. and *Tamarindus indica* L. At low and medium altitudes these species are confined to the drainage hollows and plains, where they are often associated

with grasslands. At higher altitudes in some districts they reappear scattered through the open upland grasslands on eluvial and colluvial, as well as alluvial, soils (Phot. 28). *Acacia albida* Del., for instance, which one thinks of as characteristically a tree of rich lowland valley bottoms, grows on open hill-sides at a height of 6000 ft. at Mbeya in Tanganyika. Some ecologists might consider this to be evidence that these trees are the pioneers of woodland at all elevations in colonizing open grassland, which is supposed to be an early stage

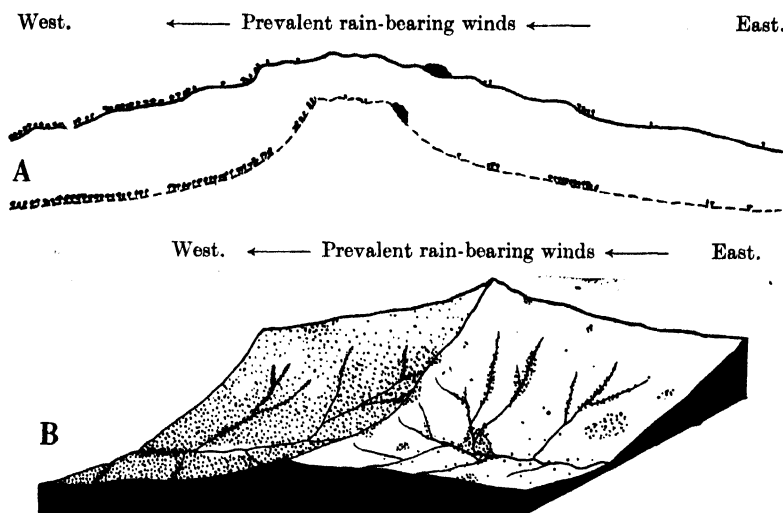


FIG. 5. Eastern border highlands, Southern Rhodesia. A. Diagrammatic section through watershed. (Outlines of crests represented by full lines, of valleys by dotted lines. Forest patches shown black.) B. Block diagram. (Trees represented by dots.)

in succession. A more satisfying explanation is that they are trees which demand a fairly rich soil with a good water supply, although they are not exacting about drainage. Their presence in upland grass areas shows that these grasslands have richer soil than areas of other types of bush and woodland adjoining them. The greater extent of richer soils in the highlands than in plateaux of lesser elevation could be explained by the smaller amount of leaching, which is due to the more continuous nature of the plant covering, the less drastic drying out and cracking of the soil in the dry season, and the greater gentleness of the rain storms.

The formation of open grasslands by climate is shown also in the alpine meadows above the tree line on the high mountains. Even here soil factors may play a part, for Scaëtta (17) finds some open, marshy areas of mixed grasses and sedges to be due to waterlogging even at these altitudes, and suggests that some of them are due to erosion of rock platforms and hollows by ancient glaciers. He also finds that the grassy patches on the mountains have usually a lower acidity of the soil than the surrounding areas, but he considers this to be effect rather than cause.

Another cause of the formation of upland grassland is destruction of rain forest by man. In fact this is often considered to be the sole origin of the whole of some of the largest areas. There are many areas where the edges of forests have receded and been replaced by open grassland within living memory. The best soils in upland regions are usually found in the forests, the edges of which are selected by natives for their shifting and by Europeans for their more permanent cultivations. Although evergreen scrub and eventually forest become re-established on abandoned gardens, each fresh clearing of a site makes recovery more difficult, as baring the soil enables much of it to be washed away.

Man is even more destructive through his fires, to which forest species are very sensitive, unlike savannah species. Besides killing the plants, the fire destroys the humous surface layer of the forest soil. Apart from deliberate burning of slashed vegetation to clear the land for cultivation, annual fires in the grasslands adjoining nibble at the forests by burning back a few feet each year (Phot. 33). In exceptionally dry years the forests themselves may catch fire and be killed for miles.

Even in the absence of fire, it is possible that the change from forest to grassland may become irreversible by the formation of ironstone pan under the surface in the secondary grassland. This suggestion was made to the writer in the Iringa Highlands of Tanganyika, where ironstone is certainly common in the grassland (Phot. 33). How far it has only been formed after destruction of forest it is difficult to say. Scaëtta (17), who considers almost all the grasslands of the central African highlands to be secondary, says that the formation of grassland indicates degradation of the soil, which in extreme cases may become irreversible. Such irreversible grasslands consist of open communities of few cosmopolitan species.

An instance where clearing causes such a pan formation, which can slowly be reversed by recolonizing vegetation, is that found by J. B. Clements in the Cypress Forests (*Widdringtonia Whytei* Rendle) on the bauxite deposits of Mt. Mlanje in Nyasaland (4).

In lowland regions repeated destruction of rain forest or of savannah is followed by the secondary invasion of savannah trees. In the uplands the savannah bush is much less aggressive. Continued clearing and burning of forest therefore result in open grassland, which is only slowly invaded by savannah trees.

In the uplands of tropical Africa there is a curious association between rain forest and open grassland. Only once in his travels has the writer seen a gradual transition between closed forest and savannah woodland, at a little kloof forest patch called Umpengu on the Portuguese Border at Eastleigh Farm, Chipinga, Southern Rhodesia (Phot. 32). Occasionally a sharp change of soil allows savannah to come up to the edge of a forest, but not to mix with it. Normally the forest ends as sharply as a wall, outside which is open grassland, with or without dotted bushes and trees.

This existence of an open gap between forest and savannah woodland is so widespread, that it suggests that it is natural and not entirely due to destruction of intervening forest by man. The sharpness of the forest edge is doubtless accentuated by fire, which can burn the grass, but which can normally only singe the edge of the forest but not penetrate it (Phot. 33). Another possible explanation is that the forest, with all its secondary developmental stages, is a closed community. It can develop as a dense mass of vegetation or not at all, most of the forest species being incapable of living in the open. There can, therefore, be no sparse fringe of dotted forest trees and bushes.

In areas of forest and grassland the forests usually occupy kloofs and valleys with richer soil and better water supply (Photos. 32, 34), or the crests and faces of escarpments facing the prevailing rain-bearing winds (Phot. 32). If the grassland were entirely due to destruction of forest by man, one would expect the boundaries between the two to be more haphazard in arrangement.

It seems possible that these upland grasslands are a hiatus between two different floras. The African closed forest flora is adapted in parts to great heat and in parts to considerable cold, but not to a very severe dry season. The African savannah flora is adapted to severe dry seasons and to great or moderate heat. It has never become adapted to extreme cold or dampness of air or soil. Although in the course of ages the rain forest and the savannah (including thicket) tree and bush floras have succeeded in colonizing most of tropical Africa and a great deal of the temperate south, yet there are certain highland areas which are too dry for forest and too damp and cold for savannah. These areas therefore remain open grassland. This theory is supported by the stunted forms of such savannah trees as venture out furthest into the grassland at high altitudes (Phot. 31).

As already mentioned, there are some places where upland grasslands contain dotted fragments both of savannah and of forest side by side. In present-day conditions of annual burning of the grass the forest clumps are usually being slowly destroyed (Phot. 33). It would be interesting to be able to study such an area and to withhold fire. It might be that results would indicate that the area had originally been forest, and that the savannah was invading the resulting grassland. It might have been originally open savannah containing solid clumps of forest type. It might have been a more diffuse mixture of forest and savannah species, or finally it might have been much as now, mainly open grass, with representatives of both dotted about in it.

Summarizing, it may be said that many upland grasslands are caused by widespread seasonal soil waterlogging. There is evidence that other soil conditions also cause the scarcity of trees, partly the lack of marked drying out during the dry season, and partly the richness chemically. Climate has an effect, both directly and through the soil. Parts of the higher grasslands are artificial and caused by destruction of rain forest by man, aided by fire. The extent of this is uncertain, and it is possible that a belt of grassland always

existed between the forest and the savannah, owing to neither flora being adapted to this particular set of conditions. If this is so, man has only widened the belt which existed already.

B. *Other soil factors.* Apart from waterlogging, indications have been given above that open grasslands at the higher altitudes are commoner on richer soils, associated with such trees as *Acacia* spp., than on poorer soils, which tend to be occupied by bush of *Brachystegia* or some other form. There are also rare instances of other soil factors, not yet understood, preventing tree growth and causing the formation of grassland at lower elevations also.

The Umvukwe Range of Southern Rhodesia, already mentioned, has a scanty growth of trees and bushes and in parts bears more or less open grassland. Henkel (5) ascribes this to the shallowness of the soil, but rocky hills of granite in the same part of the country are usually wooded with *Brachystegia*. It seems probable that the norite rock forms a soil chemically or physically unsuitable for a good growth of trees.

Robyns (1932, *Natuurw. Tijdschr.* **14**, 101-6, cited in (16), p. 85) has described clearings in the woodlands of the Haut-Katanga district of the south-eastern Congo coinciding with outcrops of copper ore.

Lebrun (7) mentions grasslands of *Tristachya leucothryx* Trin. and *Aristida recta* Franch., with bushes in rocky parts, on the residual sandy soils of a ferruginous chain of hills north of the Uele in the north-eastern Congo.

Robyns (16) discusses in detail the "esobe" of the western part of the forested Congo basin. They are of small extent and few in number. They occur along rivers, but are separated from the actual banks by gallery forest. On the other sides they are surrounded by marshy rain forest. The esobe themselves are open areas dominated by an often pure growth of *Hyparrhenia diplandra* (Hack.) Stapf. Robyns concludes that they are natural grasslands, from which the savannah flora is excluded by the very wet equatorial climate, and the forest by the unsuitable soil. He suggests that they are old sand banks cut off from the rivers and slowly being invaded from inland by the forest, as the vegetation slowly improves the inhospitable soil.

C. *Man.* Man, aided by his fires and his grazing animals, has been responsible for the formation of extensive secondary grasslands. The chief of these are parts of the upland grasslands, whose origin from mountain rain forests has already been described. At lower elevations man's activities seldom give rise to important grasslands.

In the drier regions grazing and cultivation on a large scale so weaken the tree and grass covering, that "cultivation steppe" results. This consists of country dotted more or less sparsely with trees, but with much of the ground bare in the dry season. The nakedness of the ground causes soil erosion with the early rains. This prevents the regeneration of anything but xerophytic plants. In parts, however, grassland may be formed, if tree growth is naturally sparse and grazing is not too heavy (Phot. 26).

In damper climates the savannah trees have such powers of regeneration, that their coppice and seedling growth soon recolonizes cleared areas. Over enormous areas the presence of tsetse fly (*Glossina* spp.) prevents man from keeping domestic animals, or even, by sleeping sickness, decimates the human population. Man's destructive action on the vegetation is thus greatly reduced. Even round large settlements, where the trees are kept permanently cut, there are usually so many woody coppice shoots from the cut stumps, that open grassland is not formed.

In the wettest climates, where rain forest and not savannah woodland covers the country, cleared areas tend quickly to revert to forest. There are, however, places where the influence of man is strong enough to repress the exuberant woody vegetation. It may be that the forest, especially on the fringes of its area, regenerates less readily than the moister forms of savannah bush and woodland; perhaps the richer agricultural qualities enable denser and more sedentary populations to exist locally than is usual in the less arid of the savannahs. However it may be, man is aided in this by *Imperata cylindrica* (L.) Beauv. var. *Thunbergii* Hack., a powerful, rhizomatous grass. In the lateral tropical belts this grass is confined to seepage areas and to old native gardens with an underground water supply. In the equatorial zone the continually moist soil enables it to invade any cultivated ground and exert a stranglehold on other vegetation, whether crops or the native forest trees starting to regenerate (7). According to Robyns (16) even areas covered with this grass tend slowly to return to forest, but in the northern Congo there are regions where the continued presence of man is sufficient to keep large areas under *Imperata*. In some wetter and cooler parts of the equatorial belt the same part is played by Elephant Grass (*Pennisetum purpureum* Schum.).

D. *Fire*. Many have written about the fires of the tropics, some magnifying and some minimising their destructive action on the woody vegetation. There is no doubt that their effect is very great, although they are grass fires and not forest fires. It is exceptional for whole trees to burn, though upland forests have been known to catch fire in dry seasons (e.g. Uzungwa Escarpment forest in Tanganyika).

In desert regions the grass is too scanty to burn. In the wetter but still arid savannah it is burnt in parts, but areas heavily grazed, much cultivated, or with naturally shallow soil and poor grass, break up the country and prevent it from being burnt throughout. The wetter savannah regions, with their luxuriant growth of grass, are burnt right through every year. The rain forests, having no continuous grass undergrowth, do not burn, though open grasslands in forest areas may be burnt. The grass of the equatorial belt, with its, at most, short dry seasons, does not burn as fiercely as that of the north and south tropical belts, with their single long dry seasons. This effect of climate is enhanced by the richer growth of grass in the lateral tropical zones than in the central equatorial belt (see below, § 6).

Fire favours grassland at the expense of bush and forest. Its action in turning mountain forest into upland grassland has already been described.

Dense thicket, like that of central Tanganyika (13), the Mweru-Tanganyika Lowlands of Northern Rhodesia (Phot. 13), and the gullies of the hills of Ankole in Uganda (Phot. 27), is ordinarily impenetrable by fire and therefore contains many species sensitive to it. In consequence it is liable to gradual erosion of its edges by scorching in the same way as forest. Sometimes, as in Ankole and on the ironstone pan soils of the Mweru-Tanganyika Lowlands, the ground thus won from thicket becomes partly grassland. More usually the climatic and soil conditions are such that open savannah bush replaces the thicket. This is also so with outlying patches of lowland tropical rain forest.

Ordinary savannah country is usually burnt through annually in the less arid regions. The trees and bushes of the damper savannah country are therefore all adapted more or less to regenerate after being burnt. It is difficult to say how great is the effect of fire in keeping down tree growth and forming grassland, but it is clear that continued burning back of seedlings and coppice growth does make the country much more open than it would otherwise be. Under the rule of the annual grass fire, open grassland remains open grassland, and bush remains bush, but transitional areas, which would naturally be open bush, are converted to grassland with only scattered and stunted trees and bushes.

Fire thus acts mainly in widening the boundaries of open grasslands formed by other causes already described, rather than in creating new grasslands.

It also affects the composition of the grasslands themselves, favouring the growth of grasses and geophytic herbs and undershrubs at the expense of lanker herbs and shrubs. Experiments at Lake Rukwa, to be described elsewhere, show the surprising fact that some grasses may actually be killed by not being burnt annually, and that invasion of other herbs follows, instead of causes by competition, the death of the grasses.

E. *Frost*. Henkel (5) shows how valley grasslands on the Southern Rhodesian plateau are often liable to frost, while the higher ground around does not suffer from it. He says that the effect of annual frost injury on tree growth invading the edge of the vleis is commonly seen. This effect is probably widely spread in upland regions. Although there is usually more or less air movement during much of the day, tropical African nights are commonly very still. Descending into a valley at night in the winter often feels like stepping into a cold bath.

5. OCCURRENCE OF TREES IN WATER

It has been described how most African grasslands owe their origin to prevention of tree growth by seasonal excess of water in the soil. It is therefore of interest to examine the exceptions, where trees are able to grow with their roots submerged.

The mangroves need not be discussed here, as their high specialisation is well known, and as they seldom occupy ground which would otherwise be grassland.

In the central Sudan the Sunt tree, *Acacia nilotica* DC., forms little woods on the gently sloping banks of the White Nile, where its flood waters are dammed back by the greater flood of the Blue Nile (Phot. 3), and in hollows lying behind the higher banks in the bends of the Blue Nile. The latter are not flooded naturally in years of low floods, but the valuable trees grow so much better if flooded, that ditches have been cut in the river banks to admit the flood waters every year. The ground is flooded for two or three months, but in the long months of the dry season the ground dries up and cracks very heavily.

Occasionally in Central Africa one finds lowland areas which are flooded by rivers in the rains but which bear numbers of trees of such species as *Acacia albida* Del., *A. campylacantha* Hochst., *Ficus Sycomorus* L. and *Kigelia pinnata* DC. The writer can only bring to mind two such places, both in Tanganyika. They are the Tendiga Swamp, where the River Kinyasungwi or Msoa forms a delta on running out from Kilosa onto the Mkata Plain, and the deltaic swamps of the small streams which run onto the flood plain of Lake Rukwa. These are both flooded by running water, and in both instances they adjoin typical flood plain and mbuga grasslands, where the water lies probably longer and is more stagnant.

The palms, *Phoenix reclinata* Jacq., *Borassus flabellifer* L. var. *aethiopum* Warb. and *Hyphaene* sp., often grow patchily in flood plains, and are not so markedly attached to ant-hills and raised patches of ground as the dicotyledonous trees are (Photos. 7, 8). They can evidently stand more flooding than most trees, so that it is not clear what prevents them from colonizing the flood plains more completely. *Raphia* palms also occupy waterlogged stream banks and may adjoin the "mishitu" described below.

In the middle of the swamps of Lake Bangweolo in North-Eastern Rhodesia large areas of ground are just above water in the dry season. The soil is largely pure peat, which is burnt by the natives in the absence of other fuel. Amongst the mixed lush swamp vegetation grows a bush, *Ficus verruculosa* Warb., which is dominant in parts. The general aspect of the vegetation is very like that of the English fens, where similar bushes form carr, dominating the similar grass-sedge-fern-herb ground vegetation. On the other hand the lower sand banks and the immense plains round the lake have ordinary mineral soils and open grasslands of *Trichopterya simplex* Nees and other species, with other kinds of trees and bushes dotted sparsely on rising ground and ant-hills. In spite of the immensity of the swamps, most of the channels have a strong current of water in them.

Fringing forest and bush along stream banks, which often occur where a river runs through a flood plain or small valley grassland, are liable to periodical submersion of their roots. This is not usually for long at a time, and good

drainage and aeration are provided for most of the year by the trough of the stream. In broad flood plains the flooded river bank is often higher than the ground behind and therefore only flooded for short periods by the highest floods.

In North-Eastern Rhodesia many of the plateau streams rise in peculiar little clumps of forest, known locally as "mishitu" (sing. "mushitu", literally "forest"), which may be called Springhead Forests. The only one which the writer has ever seen outside this country is a partially destroyed one at the Itheme Agricultural Experiment Station, near Iringa, Tanganyika. Species of *Syzgium* are the most characteristic trees, but the whole vegetation is quite different from anything else in the country, having strong rain-forest affinities. On hillsides the mishitu may be surrounded by savannah woodland, but more usually they grow in the middle of the head of a dambo. While the dambo around is dry in the dry season, the soil of the mushitu is perpetually wet with water which seeps out gradually or bubbles out in springs. The water is therefore never stagnant.

In the Buganda province of Uganda erosion of an old plateau has cut the country up into a maze of small, winding, steep-sided valleys. Subsequent warping in connexion with the Lake Victoria basin has lessened the flow of the streams so much, that nearly every valley contains a papyrus swamp. Fringing the swamps, and in some places occupying the whole valley floor, are often strips of forest, varying in luxuriance from a line of tangled, evergreen scrub to high, dense forest. Many of these forests grow on wet ground (Phot. 35).

Large parts of the Congo basin, especially in the low-lying western end of the forest belt, are covered with swampy rain forest. Lebrun (7) describes two varieties. Forest periodically flooded has firm ground, easy to walk on when the floods have subsided. It consists of trees relatively few in species and small in size. Creepers are large and fairly abundant, but the ground flora is confined to local groups of geophytes. Marshy forest differs in having the soil always wet and soft. Though not of great height, it is rich floristically and consists of a dense tree and bush growth, with abundant large creepers and a well developed ground layer of herbs.

Summarizing these exceptions, it appears that the abhorrence of waterlogged ground is a peculiarity of the savannah tree flora, and not of the forest. Natural open grasslands are therefore very restricted in the tropical forest region. Certain palms, acacias and other savannah trees are more tolerant of waterlogging than most. Peat is probably more suitable for bush growth than the ordinary mineral swamp soils. There is reason to believe that flooding by running water is less harmful to tree growth than stagnation.

6. CLIMATE, EVOLUTION AND SUCCESSION OF FOREST, SAVANNAH AND GRASSLAND

Two instances will be given to show how local soil conditions, here the existence of seepages of doubtless perennial cool water, may bring plant communities out of their normal climatic zones.

In Rhodesia and elsewhere trees growing near water on the plateaux are mainly of the evergreen forest group typified by *Syzygium*. In the lowlands they are the thorn-fig-palm group already mentioned more than once. Fringing the open grassland at Kamba Bay, at the south-western corner of Lake Tanganyika, the interesting find was made of the two types almost side by side. The path followed traversed a line of rich fringing forest of the lowland type, composed of fine trees of *Acacia albida* Del. and *A. Vermoeseni* De Wild., *Kigelia pinnata* DC., *Tamarindus indica* L. with *Capparis tomentosa* L. on ant-hills, *Trichilia emetica* Vahl, *Combretum mossambicense* Klotzsch and other woody creepers, tangled herbs and tall *Panicum maximum* Jacq. A little off the path was a typical Springhead Forest, doubtless marking a seepage zone. The thorny Fringing Forest was on dry ground, but such trees could not exist without a good underground water supply.

At no great distance from Kamba, in the rift valley of the River Lovu, near Lake Tanganyika, a patch of damp grass with *Themeda triandra* Forsk. and numerous bog flowers had been found a day or two before. This type of vegetation also was a surprising one to find not far above the level of the lake, which lies 2540 ft. above sea-level. It is characteristic of grasslands on the plateau 2000 ft. above.

It has been suggested above that parts of the upland grasslands owe their existence to a climate to which neither forest nor savannah have become adapted. Another interesting effect of climate is shown by a comparison of corresponding plant communities in the equatorial belt of two rainy seasons, and in the lateral tropical belts with one rainy season.

Rain forest is adapted to a climate without a severe dry season. It is best developed in the north of the Congo basin and in the coast lands round the Gulf of Guinea, where rain is heavy and falls during most months of the year. In equatorial East Africa the climate is too dry for the bulk of the country to be forested, but the two rainy seasons allow numerous forests of varied extent to exist in suitable places. Outside the equatorial zone forests are much more restricted, being confined to high altitudes and seaward facing mountains, where the long dry season is mitigated by extended and heavier rains, dry season mists and low temperatures and evaporation.

Savannah and grassland react quite differently from forest. The length and severity of the dry season do admittedly affect them greatly, deciding whether the savannah shall be dominated by fine-leaved thorny acacias, deciduous broad-leaved trees or evergreen broad-leaved trees.

The luxuriance of the growth is also affected, but not entirely as might be expected. Comparing, for instance, western Uganda with the plateaux of Tanganyika, Rhodesia and Nyasaland, one finds that that dominant grass, *Themeda triandra* Forsk., grows in a low tangled mass only about 2 ft. high in Uganda, while further south it is strong and upright and 3 or 4 ft. high. *Panicum maximum* Jacq. in Uganda is a puny thing only 4 ft. tall or less (Phot. 18), instead of the 6-9 ft. which it attains further south.

Similarly the savannah bush of Uganda is a poor thing compared with that further north or south in regions of comparable total rainfall. Acacias are there dominant in some moderately moist cool regions (Photos. 17, 18, 21, 28), which, if transported to the zone of one rainy season, would be expected to carry more luxuriant vegetation (Photos. 11, 14, 33). The great *Brachystegia* woodland formation, so important in the southern tropics, is strikingly lacking from the equatorial zone. The Combretaceous bush types of Uganda resemble only the poorer types of further south.

Lake Albert between Uganda and the Congo, and Lake Rukwa in southwestern Tanganyika have similar physiography and about the same total rainfall, yet the Rukwa valley contains rich savannah woodland and bush and a magnificent growth of grass, while Lake Albert lies amid poor arid scrub and wretched grassland. Rukwa has its rains concentrated in one strong rainy season, while rain may fall in almost any month at Lake Albert. It is evident that what are usually called well-distributed rains are badly distributed for the African savannah and grasslands. These have evolved on lines which succeed best with a long growing season, and on which a long dry season is no disadvantage.

It is this difference of evolutionary lines which causes the apparent anomaly in the Semliki and Lake Edward section of the western Rift Valley of arid scrub and grassland existing side by side with tropical rain forest.

This raises the question of the causes of grasslands in other parts of the world. The great grasslands of the temperate regions of the world are certainly not due to waterlogging of the soil. One reads of forested flood plains in Guiana and the Amazon, and of Sago swamps in New Guinea. Is waterlogging inevitably bad for all woody plants without special adaptations? Is it only bad for them in certain climates or on certain soils? Are closed forest types more adapted to waterlogging than savannah types in other continents? Or is it an evolutionary peculiarity of the tropical African savannah to be unable to grow in seasonally wet soils? If so, what can be the history of such an immense and successful flora, that hardly one of its woody members has been adapted to conditions so widely found? Were its evolutionary lines laid down at a very ancient dry period, or did its great outburst take place at the time that the Congo basin was invaded by the blown sands of the Kalahari from the south, and nearly by those of the Sahara from the north?

Some authors, notably Bews (2) and Phillips (13), consider most African grasslands as early stages in a succession towards some more complex form of woody vegetation. Some grasslands are secondary and due to the destruction of trees by man and by fire. Removal of the artificial conditions from these would usually result in reversion, or secondary succession, back to the original vegetation or a modification of it.

Most African grasslands are natural or primary. The value of the inclusion of them as early seral stages in a scheme of primary succession depends firstly on the definition of succession used. If the word is used in the sense of the school of Clements, who confine the meaning to what Tansley (19) calls autogenic succession, great care must be used. The effect of the vegetation of the grassland is, in general, to add to the soil and directly to improve its quality. It has been shown that, besides certain climatic, evolutionary and biotic factors and fire, none of which are likely to be reacted on by the vegetation, the chief factor giving rise to grasslands is seasonal excess of soil water. It will depend on the physiography whether the development of the soil of a grassland will help or impede drainage, and therefore whether succession will be towards or away from tree growth. Grasslands are mainly a result of mature topography of plains and gentle slopes. Reasons have been given for believing that in some upland regions the more open grasslands are on the richer soils. If this is true, the autogenic succession may very likely be from bush to grassland, a direction which would by many be called retrogression.

If the wider definition of succession is used, applying the word to any change or to any slow change, successions in various directions can take place, according to what factors of the environment alter. Then, of course, there will be no meaning in the unidirectional charts of succession so beloved by many ecologists.

SUMMARY

1. In the Ethiopian botanical region of tropical and South Africa open grasslands occur in all zones of climate, altitude and vegetation. They are mostly too broken up to be shown on any small scale map. Although they comprise only a small part of the continent, which is almost entirely covered with bushes and trees, where it is not desert, their total area and importance is great.

2. The distribution of open grasslands in the south, centre and east of the continent is described.

3. Grasslands are described under five heads, based on climate and physiography, (i) flood plains (mainly lowland), (ii) small valley grasslands (vleis, dambos, mbugas), (iii) upland grasslands (including watershed, plateau and mountain), (iv) cotton soil grasslands of arid country, and (v) desert grasslands.

4. The causes of the existence of open grasslands are as follows:

A. Seasonal flooding or waterlogging is the chief, being the reason for the

absence of savannah trees from the flood plain, small valley and cotton soil and from a great part of the upland grasslands. It does not work in the domain of the tropical rain forest, of which special forms occupy swampy areas.

B. Too much soil moisture for savannah trees in a moist, cool climate, even without actual waterlogging, may be a cause of some upland grasslands.

C. Other physical or chemical soil differences sometimes cause the presence or absence of upland grasslands. These may be caused by differences in parent rock or in climate. Instances of grasslands at lower altitudes being due to this are very rare.

D. Parts of the upland grasslands may occupy a climatic hiatus, to which neither the forest nor the savannah tree floras have become adapted.

E. Destruction of rain forest by man in regions climatically unsuited to savannah is the origin of parts of the upland grasslands, and of certain grasslands in the equatorial belt. Outside these two climatic regions open grasslands made by man are of small extent.

F. Fire and frost are subsidiary causes of open grassland, widening the boundaries of grasslands primarily due to other causes.

G. Desert grasslands are due to the exclusion of other plants by drought, but it is not known why in some places grasses and in some places bushes or small herbs should extend furthest into the deserts.

H. In dry climates brackish soils bear brak plants rather than grasses, but in less arid parts grasses succeed in such places.

5. Open grassland being caused by lack of trees, usually owing to waterlogging of the soil, the few exceptions in which trees have been seen growing in waterlogged soil are described. Rain forest can grow in swampy places, savannah very rarely.

6. Local soil conditions may overcome the influence of climate and cause a type of grassland or other vegetation to appear outside its normal climatic zone.

7. While the African rain forest is best developed in regions without a severe dry season, the savannah and grasslands are adapted to grow best where there is a single long rainy and a single long dry season. This raises interesting questions on the evolutionary and climatic history of their floras.

8. Grasslands are not necessarily early seral stages in the succession to savannah bush or forest. The correct succession can only be interpreted by careful study of each type individually.

REFERENCES

- (1) *Beit Air Map of Northern Rhodesia*. Salisbury, Southern Rhodesia, 1935.
- (2) **Bews, J. W.** *Plant Forms and their Evolution in South Africa*. London, 1925.
- (3) **Chipp, T. F.** "The Imatong Mountains, Sudan." *Kew Bull.* no. 6, 177-97, 1929.
- (4) **Clements, J. B.** in **Topham, P.** *Check-lists of the Forest Trees and Shrubs of the British Empire*. No. 2. *Nyasaland Protectorate*. Oxford, 1937.
- (5) **Henkel, J. S.** "Types of vegetation in Southern Rhodesia." *Proc. Rhodesia Sci. Ass.* **30**, 1931.

- (6) **Kalahari Report.** *Report of the Kalahari Reconnaissance of 1925.* Pretoria, 1926.
- (7) **Lebrun, J.** *Répartition de la forêt équatoriale et des formations végétales limitrophes.* Brussels, 1936.
- (8) **Maufe, H. B.** "Some problems in Rhodesian physical geology." *S. Afr. J. Sci.* **24**, 30-6, 1927.
- (9) **Maxwell-Darling, R. C.** "A short reconnaissance of Northern Dafur (Anglo-Egyptian Sudan) with regard to *Schistocerca gregaria* Forsk." *Bull. Ent. Res.* **27**, 71-6, 1936.
- (10) **Michelmores, A. P. G.** "Summary of results and programme of further investigations on the Red Locust, *Nomadacris septemfasciata* (Serville)." *Proc. 3rd Int. Locust Conference*, Appendix 11, London, 1934.
- (11) **Michelmores, A. P. G.** "Plan for investigation on *Nomadacris septemfasciata* (Serv.)." *Proc. 4th Int. Locust Conference*, Appendix 34, Cairo, 1937.
- (12) **Newbold, D.** "A desert odyssey of a thousand miles." *Sudan Notes and Records*, **7**, 43-83, July, 1934.
- (13) **Phillips, John.** "Some important vegetation communities in the Central Province of Tanganyika Territory (formerly German East Africa)." *This JOURN.* **18**, 193-234, 1930.
- (14) **Pole Evans, I. B.** "The Veld: its resources and dangers." *S. Afr. J. Sci.* **17**, 1920.
- (15) **Robbins, C. R.** "Northern Rhodesia: an experiment in the classification of land with the use of aerial photographs." *This JOURN.* **22**, 88-105, 1934.
- (16) **Robyns, W.** "Contributions à l'étude des formations herbeuses du district forestier central du Congo Belge." *Mem. Inst. Roy. Col. Belge*, Sect. Sci. Nat. et Méd., Coll. in 4°, **5**, fasc. 1, 1936.
- (17) **Scaëtta, H.** "La genèse climatique des sols montagnards de l'Afrique centrale. Les formations végétales qui en caractérisent les stades de dégradation." *Mém. Inst. Roy. Col. Belge*, Sect. Sci. Nat. et Méd., Coll. in 4°, **5**, fasc. 2, 1937.
- (18) **Schantz, H. L. & Marbut, C. F.** "The vegetation and soils of Africa." *Amer. Geog. Soc. Res. Series*, **13**, 1923.
- (19) **Tansley, A. G.** "Succession: the concept and its values." *Proc. Int. Congress Plant Sciences*, 1926, pp. 677-86, 1929.
- (20) **Trapnell, C. G. & Clothier, J. N.** "The soils, vegetation and agricultural systems of North-Western Rhodesia," *Rep. Ecological Survey, N. Rhodesia.* Lusaka, 1937.
- (21) **Young, R. G. N.** "An account of a botanical excursion through northern Angola." *S. Afr. Biol. Soc.*, Pretoria, Pamphlet no. 6, 1933, 25-32.

NOTE. Numbers in brackets, e. g. (T. 240), are the index numbers in the author's collection of photographs of vegetation.

FLOOD PLAIN OF LAKE RUKWA, TANGANYIKA, SOUTHERN TROPICS



Phot. 1. In a year of low flood, dry season. Mainly burnt plain of *Diplachne fusca* and *Cynodon dactylon* traversed by stream bed with *Aeschynomene cristata* and *Echinochloa pyramidalis*. 2700 ft. (T. 240.)



Phot. 2. In a year of high flood, dry season. *Diplachne* flourishing and invaded by *Typha* sp., *Cynodon*, *Aeschynomene* and *Echinochloa* dead and dying. (T. 312.)

MICHELMORE—TROPICAL AFRICAN GRASSLANDS

FLOOD PLAIN GRASSLANDS, NORTHERN TROPICS AND EQUATORIAL ZONE



Phot. 3. Grazed flood plain of White Nile, with line of Sunt (*Acacia nilotica*) trees at edge of flood plain and dry thorn bush behind. Northern Tropics. 1500 ft. (S.S. 21.)



Phot. 4. Lake Kioga, Uganda. Narrow flood plain with short *Echinochloa pyramidalis*, *Cyperus articulatus*, etc., between *Acacia Seyal* wood on left and papyrus (*Cyperus Papyrus*) and *Typha* swamp on right. Equatorial Belt. 3500 ft. (U. 13.)

FLOOD PLAIN GRASSLANDS, SOUTHERN TROPICS



Phot. 5. Tall *Sorghum* on recently cultivated ground, swampy river banks marked by paler line of reeds (*Phragmites communis*) in background, with dark trees on higher ground beyond. Lower Shire River, Nyasaland, 400 ft. (N. 39.)



Phot. 6. Narrow lawn of *Cynodon dactylon* and *Sporobolus spicatus*, caused partly by brackish soil and partly by grazing by hippos., with tall *Cyperus articulatus* (?) and *Typha* sp. at water's edge, and *Chloris gayana* with *Hyparrhenia rufa* adjoining the bush of *Combretum ternifolium* and *Dichrostachys glomerata*. The steep escarpment is clothed in dense thicket. Mweru wa Ntipa, Northern Rhodesia, 3500 ft. (N.R. 110.)

FLOOD PLAIN GRASSLANDS, SOUTHERN TROPICS



Phot. 7. Flood plain of River Chambeshi, Northern Rhodesia, end of rainy season, with trees confined to ant hills projecting above the flood, 4000 ft. (N.R. 211.)



Phot. 8. Edge of Usinge Swamps, Tanganyika, in beginning of rains. The trees (*Borassus flabellifer*, *Hyphaene crinita*, *Phoenix reclinata*, *Acacia hebecladoides*, etc.) mostly grow above flood level on the ant-hills. The country round is *Brachystegia* woodland. 4000 ft. (T. 31.)

SMALL VALLEY GRASSLANDS, SOUTHERN TROPICS



Phot. 9. Tall *Hyparrhenia* grassland on ground seasonally waterlogged. South of Mweru wa Ntipa, Northern Rhodesia, 3500 ft. (N.R. 101.)



Phot. 10. Coarse grassland of *Setaria* sp. and other grasses, with *Sesbania tetraptera* and *Dalbergia melanoxylon* on left, *Salvadora persica* and other bushes on ant-hill, in small dambo in Combretaceous Bush country at low altitude in the Lower Shire valley, Nyasaland, 500 ft. (N. 30.)

SMALL VALLEY GRASSLANDS, SOUTHERN TROPICS



Phot. 11. A typical small dambo in *Brachystegia* woodland, the source of a little watercourse, with mixed grasses of varied height and moderate density. Muchinga Escarpment, below Mpika, Northern Rhodesia, 4000 ft. (N.R. 185.)



Phot. 12. Boggy dambo with fine grasses and flowers in valley in *Brachystegia* woodland. Trees of *Syzygium cordatum* on left confined to bank of stream and to large ant-hills near it. The far slope is studded with small ant-hills. River Mwamfushi, Mpika, Northern Rhodesia, 5000 ft. (N.R. 102.)

SMALL VALLEY GRASSLANDS, SOUTHERN TROPICS



Phot. 13. An example of the low plateaux covered with dense thicket of *Bussea*—*Combretum*—*Grewia*—*Pseudoprosopis*—*Baphia* type on red soils on Katanga Sandstones, sometimes with sheets of secondary ironstone, in the Mweru—Tanganyika Lowlands of Northern Rhodesia. Open grassy patches with only dotted *Combretum macroense* and spp., *Acridocarpus katangensis*, *Vitex mombassae*, etc. are common, partly due to shallowness of soil on pan or rock and partly to destruction of thicket by man. Deeper soils have *Hyparrhenia*, shallower ones finer grasses like *Aristida*, as in picture. 4000 ft. (N.R. 96.)



Phot. 14. Large dambo with grassland creeping up sides of valley in parts, hills with *Brachystegia* Woodland, beginning of rains. Chito Mountain, Northern Rhodesia—Tanganyika border. 6000 ft. (T. 139.)

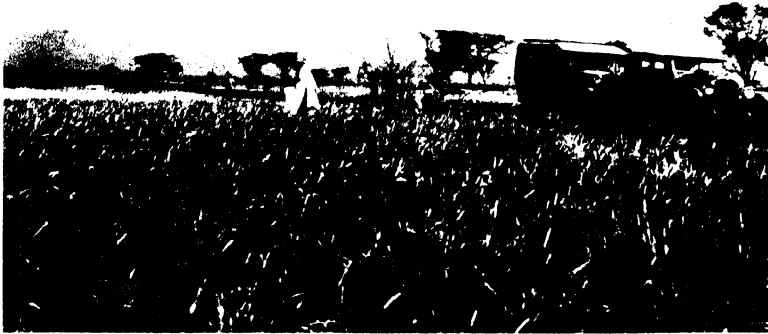
SMALL VALLEY AND WATERSHED GRASSLANDS, SOUTHERN TROPICS



Phot. 15. Similar dambo to that shown in Phot. 14, flooded in centre at end of rains. Ufipa Plateau, Tanganyika, 6000 ft. (T. 296.)



Phot. 16. Short watershed grassland with numerous herbs, low *Brachystegia* bush almost confined to hills, and a few bushes on granite rocks. Near Macheke, Southern Rhodesia, 5300 ft. (S.R. 10.)



Phot. 17. Fairly tall grassland, due partly probably to seasonally wet soil, and partly to rather dry climate with well distributed rains making thorn savannah open. *Hypparrhenia* and flowering *Imperata* growing up after burning. Dotted trees of *Acacia Sieberiana*. The cultivated top of the south east escarpment of the rift valley in the background bears elephant grass (*Pennisetum purpureum*) and remnants of rain forest. South-east of Kazinga Channel, 3500 ft. (U. 92.)



Phot. 18. Open savannah due to dry climate with well distributed rains. Grassland mainly *Heteropogon contortus* and dwarf *Panicum maximum* with *Themeda triandra* and *Sporobolus pyramidalis* (?) studded with dense clumps of *Acacia hebecladoides*, *Candelabra Euphorbia* sp., *Grewia similis*, *Fluggea virosa*, *Rhus glaucescens* and other bushes. Open plain below. Above Mohokya rest house, Lake George, 3500 ft. (U. 103.)

WEST RIFT VALLEY, EQUATORIAL ZONE



Phot. 19. Short grass plain, wet in rains, dominated by poor *Chloris Gayana*, mixed with *Sporobolus pyramidalis* forma, *Heteropogon contortus*, *Bothriochloa insculpta* and poor *Hyparrhenia filipendula*, with patch of short *Imperata* in centre by butterfly net. Low ant hills bear Candelabra *Euphorbia*, *Grewia similis*, *Azimia tetraantha* and *Cissus quadrangularis* (?). Little bushes of *Pluchea ovalis* are dotted in the grass. Mohokya rest house and wooded foothills of Ruwenzori visible behind. 3500 ft. (U. 95.)



Phot. 20. Coarse flood-plain grass on lower part of same plain. Burnt *Imperata* with *Indigofera arrecta* in open, partly burnt tall *Panicum maximum* and *Echinochloa pyramidalis* on stream banks. (U. 99.)

SMALL VALLEY GRASSLAND, WESTERN UGANDA, EQUATORIAL ZONE



Phot. 21. A temporarily flooded open grassy bottom, surrounded by rolling *Themeda* grassland, dotted thickly with *Acacia Sieberiana* and with ant-hills with *Candelabra Euphorbia*, and transitional to more open upland grasslands. Eastern Ankole, Uganda, 4500 ft. (U. 64.)

COTTON SOIL GRASSLAND OF ARID COUNTRY, SOUTHERN TROPICS



Phot. 22. A little open hollow of perennial grass fringed with the taller and looser *Acacia Seyal* var. *fistula*, in a large cotton soil mbuga densely covered with the smaller and stiffer *A. drepanolobium* forma (?) under which there is only a low growth of annual grasses and Acanthaceous herbs. But for the existence of these gall acacias such mbugas would probably be all open grassland. North of Singida, central Tanganyika, 5000 ft. (T. 58.)

ARID THORN COUNTRY, NORTH-EAST UGANDA, EQUATORIAL ZONE



Phot. 23. Patchy burnt *Hyparrhenia* grassland and sparse thorn bush of *Acacia drepanolobium* and *Balanites aegyptiaca* occupying cotton soil parts of undulating plain. *Bauhinia Thonningii* on right. North-east Teso, 4000 ft. (U. 21.)

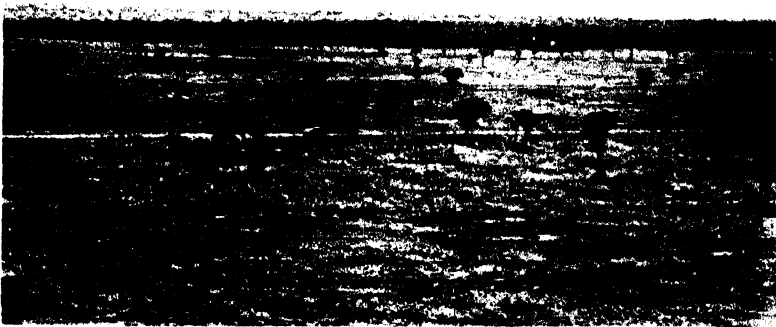


Phot. 24. Scattered thorn bush of *Acacia Senegal* with an *Aloe*, denser than in Fig. 23 because soil more gravelly, but grass of *Hyparrhenia filipendula* (?) low and sparse because of drier climate. Karamoja, 4000 ft. (U. 36.)

ARID THORN COUNTRY, NORTH-EAST UGANDA, EQUATORIAL ZONE



Phot. 25. Seasonally swampy little valley with cotton soil in the sparse thorn-grassland undulating plain. Dense 6 ft. grass probably *Echinochloa pyramidalis*, *Hyparrhenia rufa* and *Setaria* sp. *Acacia drepanolobium* and *Balanites aegyptiaca* visible. Karamoja, 4000 ft. (U. 37.)



Phot. 26. Very open parkland of *Acacia Sieberiana* in burnt *Hyparrhenia* grassland on sandy soil, partly derived from volcanic rock, with local superficial ironstone. Openness of bush probably due partly to clearing by man, partly to ironstone pan and partly owing to rich but light nature of soil excluding tree species which form denser bush on poorer or stony soils. View from Opopwa Hill towards Napak (or Kamalinga) Mountain, Karamoja, 4000 ft. (U. 23.)

UPLAND GRASSLAND, WESTERN MASAKA, UGANDA, EQUATORIAL ZONE



Phot. 27. General view of shallow-soiled grassy hills dotted sparsely with bushes, gullies with dense evergreen thicket and deeper soiled valleys with tangled vegetation of grasses, herbs, bushes and invading thorn trees secondary to such thicket. Owing to the moderate but well-distributed rainfall the savannah bush is of an arid type but the thicket has forest affinities. 4500 ft. (U. 62.)



Phot. 28. Closer view of hill covered with *Themeda triandra* dotted sparsely with *Acacia hebecladoides*, *Combretum* sp. and *Gymnosporia* sp. The lower country below is rolling grassland dotted with ant-hills bearing bushes. 4500 ft. (U. 61.)

UPLAND GRASSLAND, EASTERN BORDER OF SOUTHERN RHODESIA,
SOUTHERN TROPICS

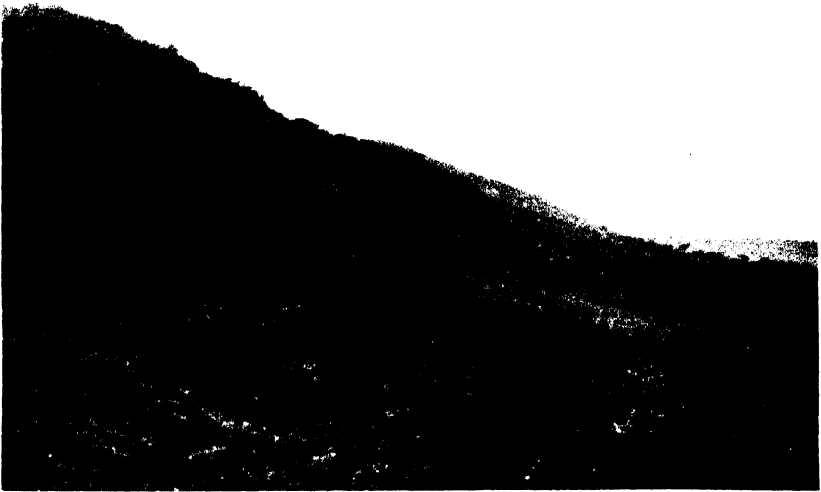
Phot. 29. View from below Msaaps Nek of east-running Msaaps River valley, open grassland with local patches of *Brachystegia* woodland. 5500 ft. (S.R. 35.)



Phot. 30. View from near Commik Nek of west-running valley occupied mainly by low *Brachystegia* woodland with some open grass. 6000 ft. (S.R. 37.)

UPLAND GRASSLAND, EASTERN BORDER OF SOUTHERN RHODESIA,
SOUTHERN TROPICS

Phot. 31. Effect of climate of high altitudes on a dominant and usually slender and graceful savannah tree of fair height, Msasa (*Brachystegia Bragei*), near Commik Nek, 6000 ft. (S.R. 36.)



Phot. 32. Small kloof forest merging into savannah woodland below. The open grass in front is partly natural tall *Hyparrhenia* grassland, with elephant grass (*Pennisetum purpureum*) on the summit beside the forest, but has partly been cleared of open savannah bush as a barrier to the advance of tsetse fly from the Portuguese country on the right. Umpengu forest patch, Eastleigh Farm, Chipinga, 3000 ft. (S.R. 16.)

UPLAND GRASSLAND, SOUTHERN TROPICS



Phot. 33. Upland grassland with grass mainly *Themeda* still short in middle of rains, showing abundance of rhizophytic herbs. Fine forest type clump dominated by a large *Parinari* sp. on the left, with two isolated fire-scarred trees witnessing its former wider extent. Across the valley on the right is a patch of sparse, stunted *Brachystegia* savannah woodland, above which are more forest clumps. The open grass itself is dotted sparsely with bushes of *Protea uhchensis*, *P. madiensis* (?), *Byrsocarpus* sp. and *Psorospermum febrifugum*, especially on the far slope near the *Brachystegia*. Sao Hill, Iringa Highlands, Tanganyika, Southern Tropics. 6500 ft. (T. 96.)



Phot. 34. Short grassland with characteristic patches and lines of scrubby hygrophilous forest dominated by *Syzygium cordatum* in hanging valleys and by streams. Dry season, Zomba Mt., Nyasaland, Southern Tropics. 6000 ft. (N. 22.)

FLOODED EQUATORIAL FOREST, UGANDA



Phot. 35. Fine swamp forest, with elephant grass (*Pennisetum purpureum*) by road on left. Entebbe District, Uganda, Equatorial Zone. 4000 ft. (U. 55.)

THE ECOLOGY OF A RAISED BOG NEAR TREGARON, CARDIGANSHIRE

By H. GODWIN, *Botany School, Cambridge*
AND V. M. CONWAY, *Westfield College, London*

(With Plate XXV and thirty-four Figures in the Text)

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I. INTRODUCTION

THE study of peat lands and their vegetation in this country has lagged much behind that in other parts of north-western Europe. In Sweden particularly, the study of these peat mires¹ has been particularly intensive, and large bodies of information exist about structure, development, hydrography, and surface ecology of the many types which have been differentiated.

Perhaps the most clearly marked of the peat-mire types is the raised bog, or raised moss, i.e. the German "Hochmoor", and the Swedish "Högmosse". The raised bog belongs to the ombrogenous mires of von Post, in which peat formation is maintained directly by the precipitation on the mire surface itself, and is independent of the access of water to it from a larger catchment area. The chief peat formers are the most oligotrophic *Sphagna*, and as the

¹ No word at present exists in English to convey the sense of the Swedish "myr", which is a term meaning both any kind of peat land, and at the same time the vegetation type characteristic of such land. It is proposed to attempt to establish the use of the English word "mire" in this general sense, as a term embracing all kinds of peat lands and all kinds of peat-land vegetation.

mire grows they form a large convex mass of peat which is, in its typical development, raised above the general level of the countryside. The centre of the bog is flat or very nearly so, but the margins constitute a steeply sloping "rand" with characteristic plant communities. Where the edge of the mire meets the hard ground of the valley-side there is an accumulation of water, drained both from the upland slope and from the rand itself. This forms a stream known as the "lagg", the waters of which are richer in bases than those of the raised bog, and which support a more eutrophic type of vegetation. The great majority of raised bogs appear to develop in glaciated valleys from the nucleus of a late-glacial lake which has undergone progressive filling by lake and fen deposits before obliteration of open water allowed the establishment of the raised bog *Sphagneta*. As the raised bog spreads and fills the valley the lagg usually becomes marginal, and takes the form of small streams flanking the bog on either side, and increasing in width and volume downstream to where they converge at the foot of the raised bog (see Fig. 1). Where the lagg is deeper, the mineral content of its water is also greater, so that towards the foot of the bog the lagg species become increasingly eutrophic, and the communities increasingly resemble those of fen (Swedish "karr"). It is the mineral content of the water of the lagg which arrests the tendency of the raised bog to extend radially, through the inhibiting effect of the high mineral content of the water. Thus the extension is most severely limited at the foot of the bog, and is most active at the head, where the lagg is feeblest; correspondingly, the rand is steepest and highest at the foot of the bog and less well marked at the head.

Strictly speaking, the term "lagg" should be limited to the region between the raised bog and the hard ground of the valley side, but in many instances one side of a raised bog will be found to be limited by a river or stream flowing past the bog from the higher parts of the valley. Where this happens the lateral growth of the bog is checked and a steep rand develops, abutting sharply against the flood plain of the river.

As might be expected in ombrogenous mire, the development of raised bogs is strictly controlled by the conditions of precipitation and evaporation. They have been shown in Sweden to have fairly close climatic limits, and Osvald has shown that varieties of raised bog can readily be distinguished from the centre and from the Atlantic and continental sides respectively of the distribution area. On the continental side, as in the east of Sweden with a rainfall

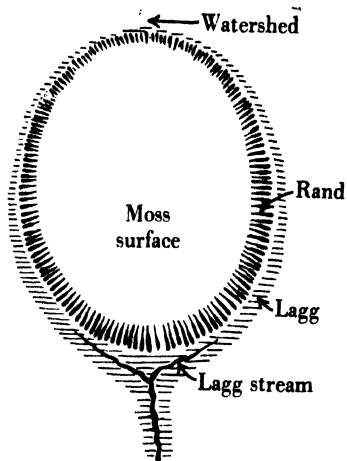


FIG. 1. Schematic representation of raised bog structure. (After Osvald, 1937.)

of about 22 in. (56 cm.), the wooded raised bog develops. It has a strongly marked rand and is more or less densely wooded, particularly on the rand: this bog type is widespread in eastern North America. On the Atlantic side of the distribution area the raised bogs are displaced by the so-called "blanket bog" (Täckmosse), which extends as a uniform blanket of peat over slopes which, in the extreme west of Ireland, may be as great as 15°. This also is an ombrogenous type of mire. It is natural that on the Atlantic side the raised bogs should acquire some of the characteristics of blanket bogs. This is well shown in the so-called "flat raised bogs" described by Osvald, in which the tendency for peat growth to extend up the sloping valley sides causes the boundary between the bog and the valley side to be very poorly marked. There is a very weak rand or none, and the lagg is very feebly developed. The peat covering and podsolization of the hill sides contribute to the mineral deficiency of the lagg. The absence of the rand near the hill side does not, of course, preclude a steep margin where such a bog is limited by a river course.

Although mires of one type and another are abundantly present in the British Isles, very few studies have been made of them, and, in particular, no raised bog has been thoroughly described. This is especially deplorable, since the most instructive examples of raised bogs in England and Wales have been so grossly exploited for peat cutting and so much burned, that few of them retain anything of their natural plant cover. Former raised bogs now quite derelict include the Somerset moors such as Shapwick Moor and Meare Heath, Thorne Waste near Doncaster, Yaxley and Woodwalton Fens near Peterborough, Fenn's Moss near Ellesmere, Shropshire, Chat Moss and Carrington Moss over which Manchester is rapidly extending, and Roudsea and Foulshaw Mosses in the south of the Lake District.

For this reason there was a particular interest in investigating the group of three large raised bogs in the valley of the river Teifi, Cardiganshire: one of these proved to be still covered with natural vegetation and to have suffered little from cutting and burning.

The bogs were investigated by Summer Excursions under the leadership of H. Godwin during the summers of 1936 and 1937. By the courtesy of Prof. L. Newton and the University authorities the Department of Botany of the University College, Aberystwyth, was placed at our disposal, and we are very grateful for the kindness and facilities given us there. We should like also to thank Lord Lisburne for giving us access to the bogs and Mr I. Jones for giving meteorological information.

The parties of investigators consisted of the following members: H. Godwin, V. M. Conway, M. Fearnside, M. A. Keay, J. Scholes, M. H. Clifford, E. Stokes, K. M. Jones, B. H. Wright, C. H. Brown, J. S. Turner, D. H. Valentine, H. R. Ross, and P. Hugh Jones of Cambridge, K. B. Blackburn of Newcastle, H. A. Hyde, F. J. North and A. G. North of Cardiff, G. F. Mitchell of Dublin,

E. Canton, H. Edwards, J. B. Jones, G. Davies, E. H. Chater of Aberystwyth, T. G. B. Osborn of Sydney, and E. W. Jones and A. R. Clapham of Oxford.

We had the invaluable assistance for one day of Prof. H. Osvald's company and advice. Dr Salter gave us valuable help with the identification of flowering plants, and we are much indebted to Dr Sherrin for identification of *Sphagna*.

II. SITUATION AND CLIMATE

About 15 miles south of Aberystwyth, the river Teifi runs south through a glaciated valley about 1 mile in width. Part of the work of the expeditions was to establish the stratigraphy of the raised bogs and to discover the nature of their developmental history (Godwin & Mitchell, 1938). This work showed that a large complex of bogs developed over a late-glacial lake which was formed behind the extensive end-moraine on which the village of Tregaron now stands, and through which the Teifi is cutting a narrow outlet channel. In this complex three large raised bogs are clearly recognizable (Fig. 2). The two on the eastern side of the Teifi are separated from one another by a ridge of high ground, have been extensively cut, and have suffered recent burning. For this reason their surface ecology has not been dealt with, but the south-eastern bog lent itself very readily to stratigraphic investigations: despite cutting its profile shows the characteristic shape and structure that have come to be associated with raised bogs in general. The raised bog to the west of the Teifi was much the largest of the three. It had suffered some peat cutting on the west and north margins but presented, nevertheless, long stretches of unmodified bog margin next the river, and had not, apparently, been recently burned. For these reasons it is this western bog which was made the subject of the detailed investigations recorded in this paper. Between the west bog and the two eastern bogs flows the Teifi, and the party has good reason to know that following heavy rains the river rises very rapidly and floods the narrow plain between the raised bogs. No doubt the progressive growth of the raised bogs has tended to restrict more and more the passage of the flooded Teifi, so that despite artificial straightening of the channel, the valley floor above the head of the raised bogs is a vast quagmire. It is covered with wide mats of more or less floating vegetation of markedly eutrophic character.

The general disposition of the bogs in the glaciated valley bounded by wooded or cultivated hill sides is well shown in Pl. XXV, phot. 1. The course of the river between the raised bogs shows several features of considerable interest, particularly in the formation of a series of wide shallow lakes which may possibly have been connected in some way with the confluence of tributary streams. In view of the way in which climate controls the distribution of raised bogs and the questions of the relation of these Welsh bogs to similar

bogs in Ireland on the one side and England on the other, it is important to record what is known of the climate. Unfortunately, the nearest stations are

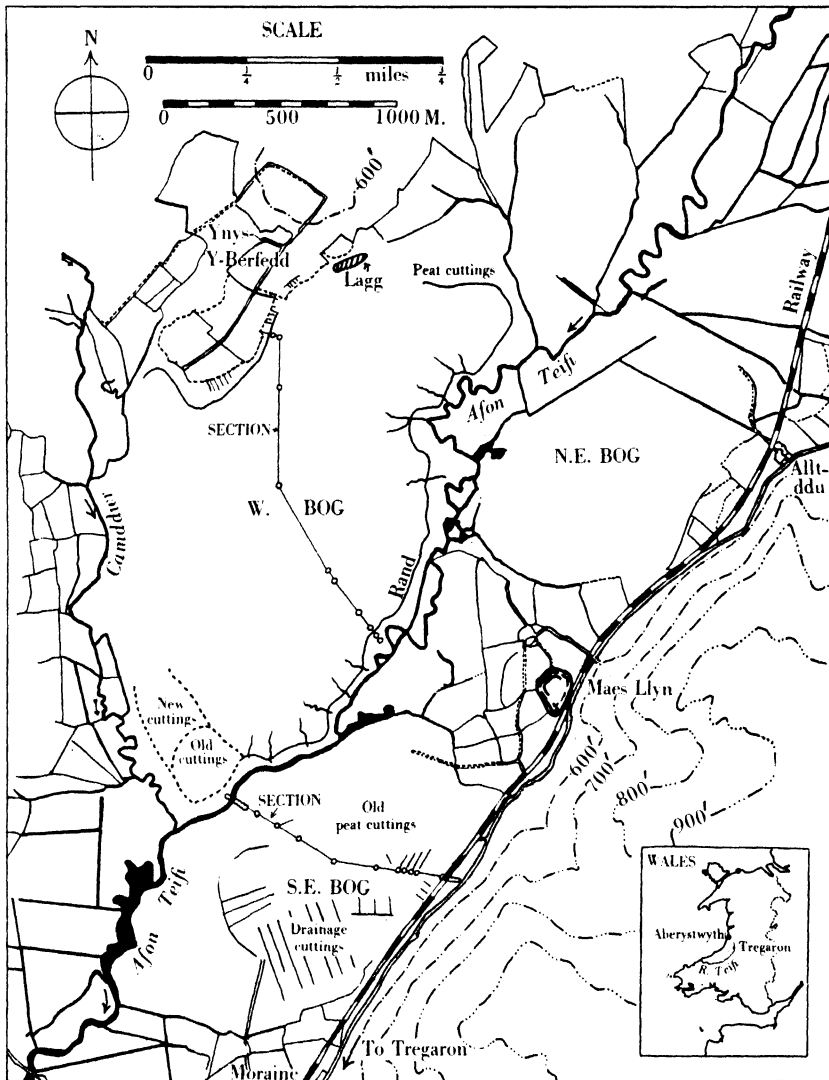


FIG. 2. Sketch-map of the Teifi valley showing the meandering river and the large raised bogs. Across the south-eastern bog and the western bog are shown the lines of section made by borings and profiles. (By courtesy of the *New Phytologist*.)

those at Aberystwyth and at the hill station of the Welsh Plant Breeding Station. The results of rainfall from the Llety-evan-hen Station and of rainfall and evaporation from Aberystwyth are given below.

Rainfall and evaporation—average per month

	Rainfall (in inches)		Evaporation (in c.c.)
	1 Aberystwyth (Plant Breeding Station)	2 Llety-evan- hen (Hill Station)	3 Aberystwyth (Plant Breeding Station)
January	4.02	4.37	2.01
February	2.78	2.44	2.22
March	2.10	2.09	2.90
April	2.05	2.41	3.77
May	2.65	2.48	5.09
June	3.43	3.87	4.44
July	3.74	4.35	5.33
August	4.31	4.62	4.85
September	4.04	4.00	4.63
October	5.46	6.12	3.35
November	4.55	4.76	2.41
December	4.07	3.96	1.57
Average for the year	43.20	45.47	42.57

(1) Aberystwyth, altitude 452 + 3 ft. The average figures given above cover a period of 12 years, viz. 1 August 1924 to 31 July 1936.

(2) Llety-evan-hen, altitude 950 ft. (approx.). The average figures given cover a period of 9 years, viz. 1 August 1927 to 31 July 1936.

(3) Average daily evaporation per month as recorded by the Piche's Evaporimeter (1 April 1933 to 1 April 1936) in c.c.

It should be noted that the altitude of the Tregaron bogs is about 540 ft. o.d. (164 m.).

III. METHODS

The western bog was over $\frac{3}{4}$ mile (1 km.) wide and about $1\frac{1}{2}$ miles (2 km.) long. This great size necessitated the use of special methods of survey and description.

After preliminary general surveys specific groups of people were given the task of investigating the communities of the *rand*, and they proceeded by making levelled transects, along which percentage cover was estimated at intervals. Another party dealt with the *lagg*, but most of the party were occupied with detailed mapping of quadrats of 1 sq. m. or 25 sq. m. selected so as to be representative of characteristic communities of the bog surface. Some of these are illustrated. As soon as it was apparent that there was a regular although complex distribution of communities on the bog surface it was clear that some general record of the entire area must be made. This was begun by setting out a base line 1900 m. long parallel to the long axis of the bog, and using this to set out a grid of squares each with sides of 100 m. By levelling all the stations on the grid it was possible to construct a contour map of the bog (Fig. 3). In § VI it will be seen that the grid was employed as the basis for a series of transects, 100 m. apart, across the greater part of the bog surface. As will be described later, the recording of these transects was specifically designed to allow the correlation of features of presumed ecological importance with position of the bog surface and relation to its contours.

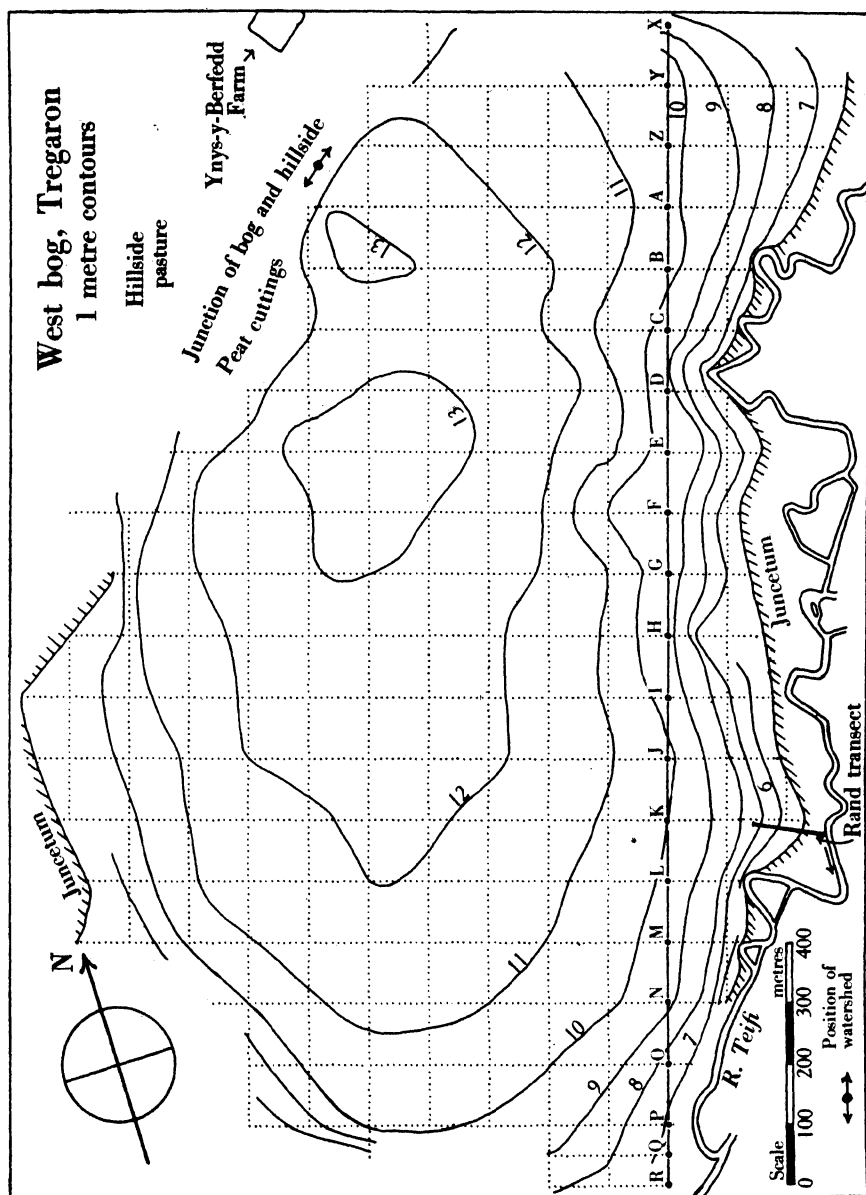


FIG. 3. Contour map of the bog showing the "grid", on which the survey of the bog is based. Posts on the base line of the grid are indicated by letters.

IV. MORPHOLOGY OF THE WESTERN BOG

The contour map (Fig. 3) gives a clear indication of the shape of the western bog. It is markedly convex with the upper surface rising more than 8 m. above the level of the river terrace of the Teifi. The eastern margin of the bog is intact along almost its entire length, and it will be seen that where it meets the flood plane of the Teifi the rand is steep and is drained by numerous small channels. Only the most important of these have been included in Fig. 2. They originate at the top of the rand on surfaces with a slope of about 1° , in a series of shallow, loosely linked bare pools, which after rain can be seen to carry flowing water. Where these channels cross the rand they are overgrown with vegetation, and do not appear to be eroding: when they meet the river terrace they disappear into diffuse waterlogged areas. Here and there at the foot of the rand there is a small pool which appears to be maintained by subterranean drainage from the bog. The southern, south-western and northern margins of the bog have been subject to some peat cutting, the effect of which has been to remove the natural rand and to drain the neighbouring parts of the bog surface. It has in particular, given a steepened run-off to marginal streams, so that, on the south-west especially, large areas are being rendered bare by the early stages of water erosion. Close to the peat cuttings on the west side of the bog the peat has here and there developed conspicuous rifts parallel with the bog margin. These are often 1 m. wide and several metres long and are filled with water. They represent, no doubt, a tendency for the damaged bog margin to burst. At the northern end of the bog the peat cuttings are older, and it is a moot point how far they are responsible for the character of the northern portion of the bog surface. This is now dissected by a close network of deep streams which are separated by irregular hummocks some 2-5 ft. high (0.6-1.5 m.). There is a great deal of bare peat exposed and erosion must be considerable: it corresponds with the Still-stand Complex of Osvald.

At the north-western margin the bog meets a shoulder of high ground on which are situated several farms, the nearest being Ynys-y-berfedd. To the south-east of this farm there is a stretch of about 600 yd. (550 m.), where the bog margin has been little enough disturbed to allow the natural form to be made out. The bog here develops no rand, but passes smoothly on to the hill side. A thin peat deposit slopes slightly up the hill. Slightly to the north of this, where a gentle rand has formed, there is developed between the hill side and the bog an area of lagg which is in an almost natural condition. In rainy weather water accumulates here, but there is normally no open water visible and a thin scrub of birch and willow grows over it. Although this lagg has been slightly drained, it is interesting to note that the ground surface in it is only 2.4 m. below the surface of the highest part of the undisturbed bog. The poor expression of the rand in this region and the absence of a well-developed lagg

stream strongly suggest that the bog belongs to Osvald's type of "flat raised bog" characteristic of Atlantic climates.

The main part of the bog surface has a very uniform character with a physiognomy simply dependent on the nature of the prevalent vegetation, in *Scirpetum* and *Molinietum* fairly sward-like and devoid of open pools, but in the regeneration complex broken by an alternation of low *Sphagnum* hummocks and shallow pools. Nowhere on the bog surface are there large streams, pools or swallow holes such as are often met with in the Irish raised bogs, although irregularities in the distribution of clumps of stunted birches suggest that such surface-drainage features may have existed formerly.

V. VEGETATION

The surface of the large western bog does not bear a uniform association of species, but a number of distinct communities. Though the species lists of many of these would seem much alike, and though the transitions from one community to another are sometimes very gradual, yet it is possible to recognize their real differences in character and to establish certain features by which to distinguish them.

Fig. 4 shows the main communities which have been recognized and their approximate position on the bog surface. It shows also the base line of the "grid" which was used in locating as exactly as possible the extent of the communities. The boundary line on the north-west and south-west margins of the bog represents the inner edge of peat cuttings. On the eastern or river side of the bog a line has been drawn to show the margin of the bog surface proper, i.e. the base of the *rand* vegetation. Between this and the river lies the "River terrace" vegetation which does not, strictly speaking, form part of the bog.

Although, as the figure indicates, the plant communities are not separated by sharp ecotone lines, the map was based on the grid survey and is of a more accurate nature than a mere sketch map derived from qualitative observations. Before it is possible, however, to describe the methods which led to this knowledge some description of the communities is necessary.

A. *Lagg*

On the sides of the bog which are not adjacent to the river, the natural margin has been almost completely destroyed by peat cutting. There is one small area left at the extreme north-west corner, which is recognizable, both from topography and vegetation, as the *lagg*. Even here there has been some peat cutting, with consequent formation of artificial ditches between the *lagg* and the beginning of the bog slopes, but the *lagg* vegetation does not appear to have been much disturbed. This *lagg* region is about 200 m. in length, and a third to a half of it bears a low scrub resembling the "Carr" of the East

Anglian fens. The canopy varies in density, and in places is closed, but here and there the bushes are younger and more scattered in the general marsh vegetation which constitutes the herbaceous layer. The ground is for the most part very wet, with the water table close to the soil surface, and in some parts it is soft and quaking.

Salix cinerea (8 or 10 m.) is the dominant tree. Epiphytic mosses are common on the lower 2 ft., while higher up lichens are numerous. Well grown specimens of *Betula pubescens* also occur, but they tend to keep to the margin of the woodland patches; they bear few epiphytes. Of the herbs, *Menyanthes*

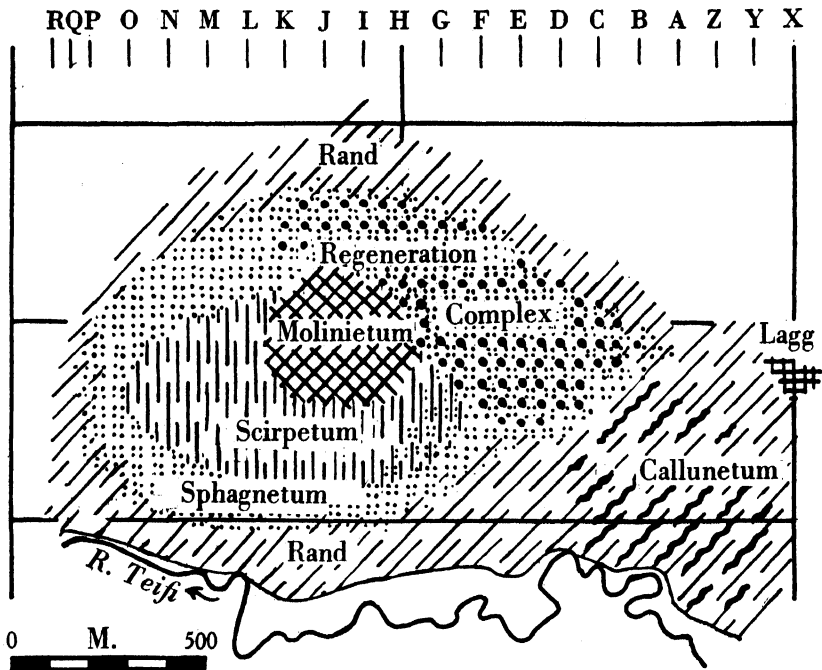


FIG. 4. Diagram to show the distribution of the major plant communities of the bog. Letters indicate the positions of the grid offsets.

trifoliata is perhaps the most characteristic, *Molinia* is abundant where the ground is slightly higher or drier, while *Juncus effusus* is more predominant in wetter parts and alongside the ditches. It seems difficult to recognize distinct communities and species lists are therefore given for the region as a whole.

The following species are frequent to abundant:

Viola palustris
Lotus uliginosus
Comarum palustris
Hydrocotyle vulgaris
Scabiosa succisa
Menyanthes trifoliata
Betula pubescens

Salix cinerea
Juncus effusus
Carex goodenovii
Holcus lanatus
Molinia caerulea
Sphagnum papillosum

The following species were present but not abundant:

Ranunculus flammula	Pinguicula vulgaris
R. repens	Prunella vulgaris
Caltha palustris	Scutellaria minor
Cardamine sp.	Salix repens
Polygala vulgaris	Orchis ericetorum
Hypericum elodes	Habenaria bifolia
Ilex aquifolia (seedling)	Narthecium ossifragum
Rubus fruticosus agg.	Juncus acutiflorus
Potentilla erecta	Luzula campestris
Sorbus aucuparia (up to 8 ft. high)	Potamogeton polygonifolius
Crataegus sp. (2 ft. high)	Eriophorum angustifolium
Drosera rotundifolia	Carex pulicaris
Epilobium sp.	C. canescens
Galium palustre	C. panicea
Cnicus palustris	C. stellulata
Oxycoccus quadripetalus	Anthoxanthum odoratum
Erica cinerea	Agrostis palustris
Fraxinus excelsior (seedling)	Deschampsia flexuosa
Myosotis sp.	Poa sp.
Veronica scutellata	Athyrium filix foemina
Pedicularis sp.	Aspidium spinulosum
Rhinanthus sp.	A. dilatatum

BRYOPHYTA AND LICHENS

Trunks:

Bases:

Eurhynchium praelongum	Mnium hornum
Dicranum scoparium	Plagiothecium denticulatum
Hypnum cupressiforme var. ericetorum	Lophocolea bidentata
Peltigera canina	

Upper parts of trunks:

Hypnum cupressiforme vars.	Cetraria glauca
filiforme and resupinatum	Evernia prunastri
Orthotrichum affine	Parmelia physodes
Ulotia crispa	P. saxatilis
Ulotia phyllantha	Usnea florida
Frullania dilatata	

Decaying stumps:

Mnium undulatum	Lophocolea bidentata
Eurhynchium praelongum	L. heterophylla
Mnium hornum	Etc.

Ground:

Brachythecium rivulare	f.	Chiloscyphus pallescens
Hypnum cuspidatum	f.-a.	Sphagnum plumulosum, green form f.
Mnium punctatum	f.	Sphagnum squarrosum v.r.
Pellia epiphylla	a.	

B. River terrace

The "river terrace" vegetation covers a much more extensive area and shows a zonation of communities in a direction parallel to the river.

(1) The actual river bank bears a tall growth of *Phalaris arundinacea* and *Deschampsia caespitosa*. This zone is not more than a few yards across.

(2) A community dominated by *Juncus effusus* occupies a wide belt.

In it occur patches of *Salix cinerea* bushes recalling the previously described lagg area. Full species lists were not obtained but the following were recorded:

Ranunculus acris
Cardamine pratensis
Galium palustre
Rumex acetosa
Carex acuta

C. goodenovii
Molinia coerulea
Equisetum sp.
Sphagnum papillosum

Carex acuta, *Ranunculus acris*, *Rumex acetosa*, and *Equisetum* were not recorded for the lagg area. *Molinia* increases in frequency as the bog margin is approached, making a transition to the third community.

(3) Here *Molinia* is dominant, accompanied by an abundance of *Comarum palustre*. Other species recorded were:

Caltha palustris
Viola palustris
Scabiosa sp.
Vaccinium vitis idaea

Agrostis sp.
Equisetum sp.
Hypnum cordifolium

Fig. 5 gives the results of a belt transect 1 m. wide taken from the river bank up to the main bog surface, and it illustrates this zonation on the lower flat river terrace. The method used was to estimate percentage cover by different species on each square metre along the transect. Species of very low frequency are indicated in the figure by a horizontal line.

C. Rand

This name is given to the most steeply sloping marginal region of the bog, but it covers two rather distinct plant communities with a transitional region between them which varies in width according to the general slope along any particular part of the rand. The species present on the rand are members of the bog flora taken as a whole, so that there is a marked contrast in passing from the river terrace or lagg on to the rand. This is well shown by the transect given in Fig. 5.

The lower of the two rand zones is a *Molinietum*, and is poor in other species. It is traversed by occasional drainage channels, and these may be wide and rather deep, but are nearly always filled with vegetation, more especially with *Eriophorum angustifolium* and *Molinia*. *Potentilla erecta* is common in this association and *Vaccinium myrtillus* occasional.

Slightly higher up the slope *Calluna* appears and may in places form a well-defined upper limit to the *Molinietum*, *Scirpus caespitosus* enters at this level, and as the *Molinia* becomes less frequent the upper rand zone is reached. Here the drainage channels are more numerous and narrower, as they have not yet coalesced to form the larger channels that traverse the *Molinietum*. Drainage channels cannot always be traced right out to the bog margin; quite frequently they fade out entirely on entering the *Molinia* zone of the rand.

The upper rand vegetation varies considerably in places, particularly in the relative abundance of *Scirpus* and *Calluna*. Where the drainage channels

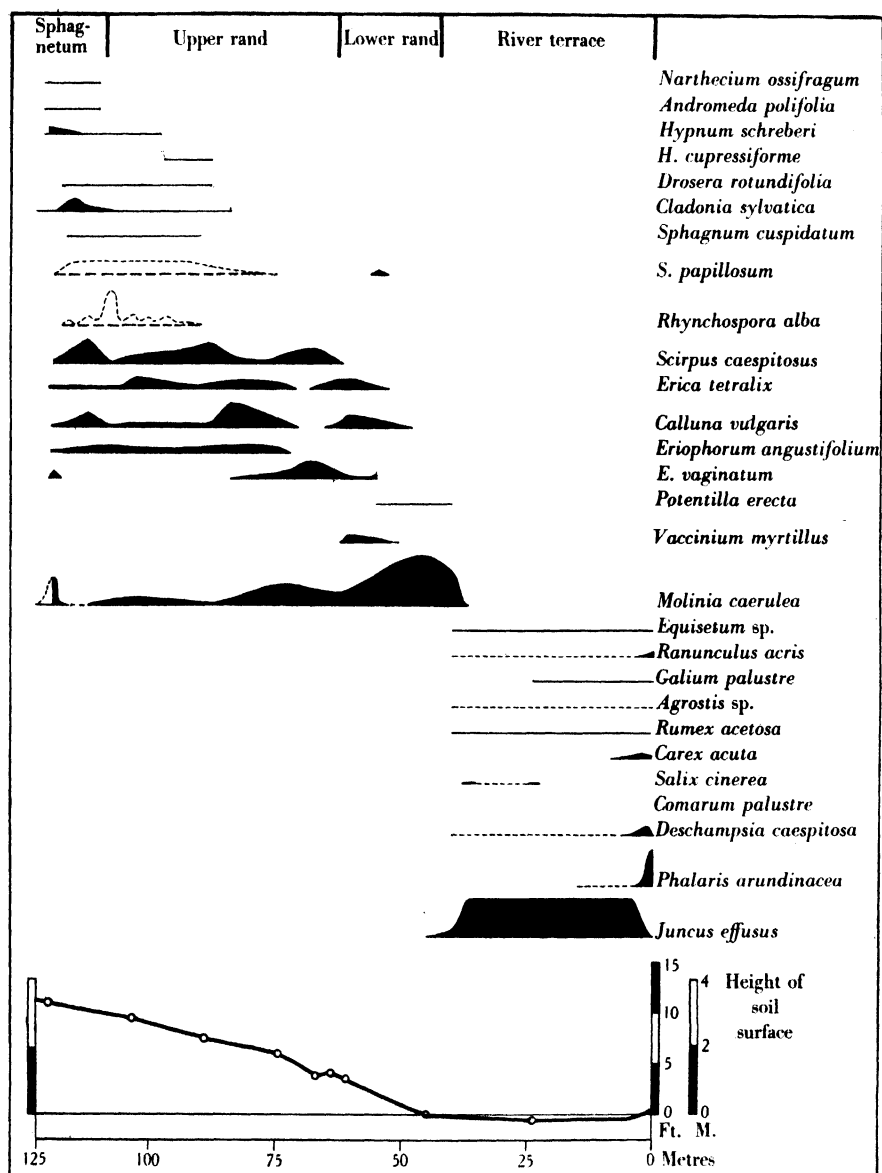


FIG. 5. Results of a belt transect 1 m. wide from the river bank across the rand. Estimations of percentage cover by the different species were made for each square metre. Dotted lines indicate the frequency of a species in the neighbourhood when it does not occur in the transect (Eastern end of offset line K of the grid, see Fig. 3.)

are numerous and the ground rough, *Calluna* takes on a bushy growth, and *Cladonia sylvatica* is conspicuous. Elsewhere *Scirpus* is more abundant and may give the region a resemblance to the Scirpetum of the main bog surface, though the latter is separated from the rand by a belt of Sphagnetum.

Betula pubescens is a rather frequent component of some parts of the upper rand, widely scattered bushes of all sizes up to 15 ft. high being present. *Eriophorum vaginatum*, *E. angustifolium* and *Erica tetralix* are the other abundant species. Patches of *Sphagnum papillosum* and *S. plumulosum* are frequent also, and it is exceedingly hard to find any boundary between the upper rand and the Sphagnetum. This is emphasized also by the presence of pools in the upper rand, scattered between the drainage channels and often linked together to form a drainage system, leading into the head of an actual drainage channel.

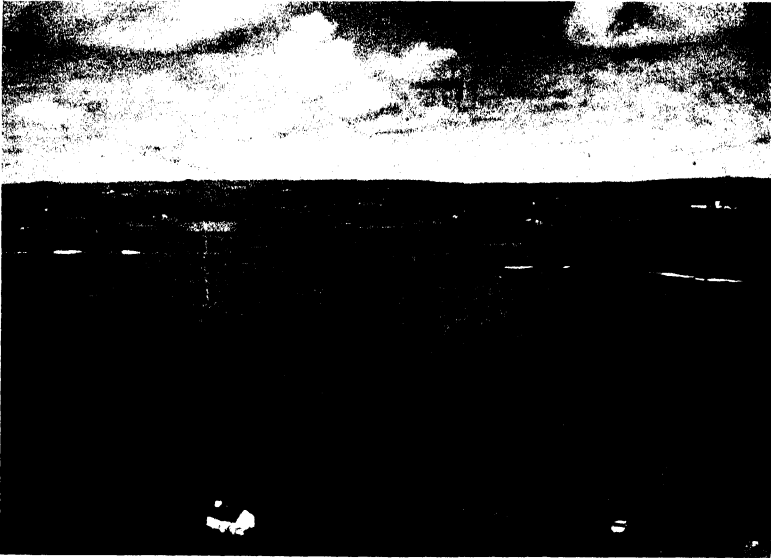
Such pools are usually shallow (10–15 cm. in depth) and have a fairly firm floor. They bear no vegetation, or only a sprinkling of *Rhynchospora alba* plants. Pools of this type are common also in the Sphagnetum, and the change from upper rand to Sphagnetum is expressed mainly in the loss of distinct drainage channels and the gradual increase of species such as *Narthecium ossifragum*, *Drosera* sp., etc., which are more characteristic of the main bog surface.

D. *Sphagnetum* and Regeneration Complex

These communities are characterized by abundance and active growth of *Sphagna*. Not only are they visible as the surface covering of the ground over a considerable fraction of the area, but they constitute the field layer in those places where other genera appear to be the local dominants. The ground is uneven since there are numerous pools or pans, and between them the vegetation is built up into low mounds and tussocks of irregular shape. The best defined and most typical facies of the community is the Regeneration Complex.

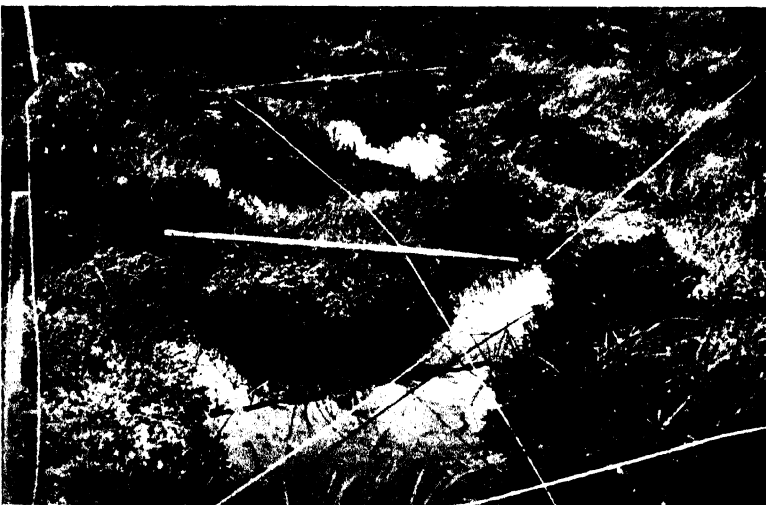
The mosaic of plant associations or subassociations which cover the ground here can only be interpreted in terms of local cycles of succession in which *Sphagnum* species colonize the bare mud of pools, and grow rapidly to build up the surface till it is dry enough to bear *Calluna*, thus preventing further growth of *Sphagnum*. Lichens, especially *Cladonia*, come in at this stage, which is followed by a breakdown of the raised tussock, leading to the reformation of a depressed area, so that a pool appears in the middle of the tussocks that have meanwhile been building up around it.

Whether the pools contain free water or not depends on weather conditions. *Sphagnum cuspidatum* may be found flourishing in the free floating condition, but evidently endures intermittent exposure on the mud surface which results from dry weather. On the other hand, the *Sphagna* that follow later in the succession occupy slightly higher slopes where complete submersion is likely to be an exceptional condition.



Phot. 1. View from the hillside above Maes Llyn cottage, looking west over the valley. In the middle foreground is the south-eastern bog, much scarred by peat cuttings; in the middle distance is the south end of the west bog covered with cloud shadows; between the two is the glint of the R. Teifi, and in the distance are the fields and farms of the hillsides across the valley.

H. GODWIN.



Phot. 2. View in the Regeneration Complex showing the alternation of pools and hummocks. The lath on the central hummock is 1 m. long. This tussock shows a well marked growth of *Sphagnum* at water-level, and to the right of it, below the diagonal tape, is a young growing *Sphagnum* hummock. Dark bushes of *Calluna* are visible on some hummocks and paler *Erica tetralix* on others.

J. SCHOLES.

GODWIN AND CONWAY—ECOLOGY OF A RAISED BOG

The pools vary in shape and occasionally form an irregular network. They are from 50 to 200 cm. across and most of them are soft and treacherous. The ground-level between the pools does not often rise more than 40 cm. above the pool bottoms; the slope from the pool edges to the highest ground may be steep but is more often gradual. The two profiles given in Fig. 6, *c*, *d* were obtained with an Abney level along lines 5 m. in length, and illustrate the nature of the bog surface, although with a much exaggerated vertical scale.

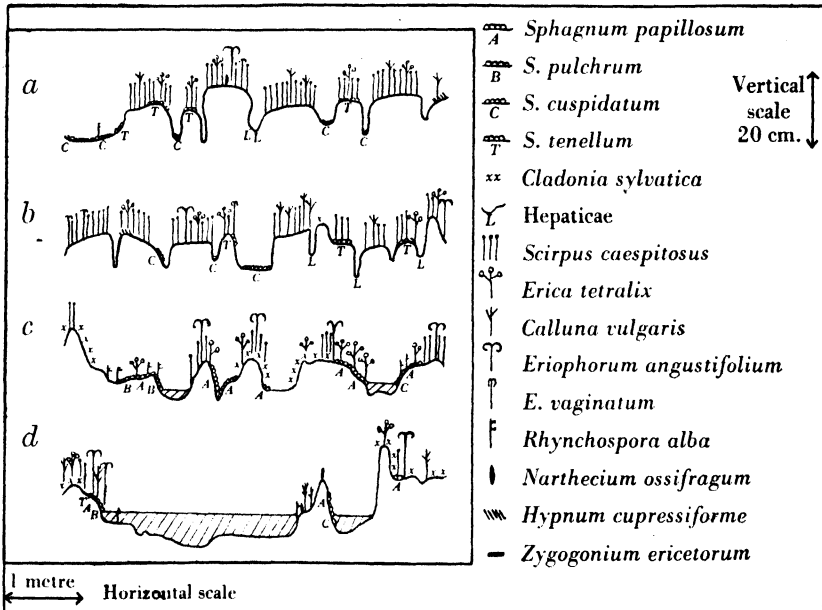
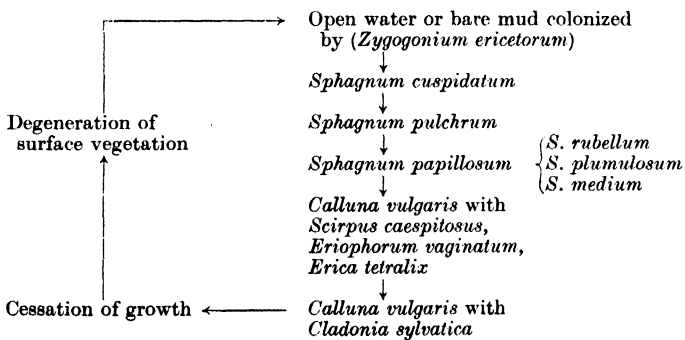


FIG 6. Levelled line transects, (a) and (b) in *Scirpetum*, (c) and (d) in *Sphagnetum*. The vertical scale is much exaggerated. The vegetation is not drawn to scale.

The ideal cycle at Tregaron may be represented in this way:



The cycle given above cannot be demonstrated clearly in more than a few spots, the degradation stages being particularly hard to find, but it does at

least give the species which are most characteristic. Although it is hard to find evidence for the view, the impression is obtained that the bulk of the peat that is formed is due to *Sphagnum papillosum* and that *S. pulchrum*, though abundant and characteristic, is not the main bog builder.

The following are associated with the early stages of the cycle, before *S. cuspidatum* has formed a closed covering:

Rhynchospora alba	f.	Drosera anglica	f.
R. fusca	o.	D. rotundifolia	o.
Drosera longifolia	f.		

associated with a rather more dense growth of *Sphagnum cuspidatum* at the pool edges are *Cephalozia bicuspidata* and *C. connivens*. The firmer substratum offered by the sloping banks of *Sphagnum pulchrum* and *S. papillosum* carries a number of low-growing, creeping species listed below, which are characteristic of this stage. There occur in addition isolated tufts and seedlings of *Calluna*, *Erica*, *Eriophorum* spp., etc., outliers of the association of the more raised ground surfaces.

Drosera rotundifolia	f.	Sphagnum medium	o.
D. longifolia	r.	Campylopus flexuosus	o.
D. intermedia	o.	Lepidozia setacea	f.
Oxycoccus quadripetalus	f.	Leptoscyphus anomalus	o.-f.
Andromeda polifolia	f.	Odontoschisma sphagni	f.
Narthecium ossifragum	f.		

The differentiation in habitat between the *Drosera* species is worth noting, *D. rotundifolia* occupying the driest, *D. longifolia* the wettest habitats of the three. Important also is the presence of *Sphagnum medium*, since this species is the main peat builder in many other raised bogs. That it does not play this part at Tregaron is evidently due to local conditions and not to the chance absence of parent plants.

The following species are associated with the raised *Calluna* associations:

Sphagnum rubellum	}	Each of these may form conspicuous "moss hummocks"
S. plumulosum		
Rhacomitrium lanuginosum		
Leucobryum glaucum		
Sphagnum tenellum	r.	Diplophyllum albicans
Hypnum cupressiforme		Odontoschisma denudata
Calypogeia trichomanis		
Cladonia rangiferina	}	Associated with the early stages of degradation
C. uncialis		
C. pyxidata		

Fig. 7 shows a mapped quadrat 5 m. square taken in the most typical regeneration complex which could be found. The mapping was carried out by eye for each square metre in turn and illustrates many of the points mentioned.

Fig. 8 is a more informal sketch which may convey a clearer visual picture of the region. It illustrates a spot where *Sphagna* are very actively filling up the depressions in the ground.

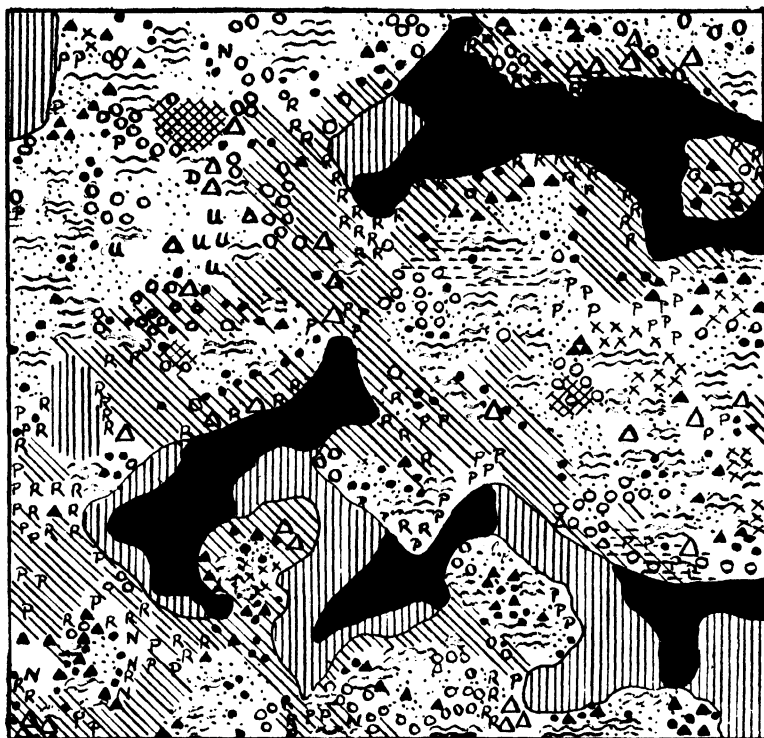



























FIG. 7. 5 m. quadrat in Regeneration Complex vegetation. (Quadrat I, position C, 520.

QUADRAT SYMBOLS

	<i>Sphagnum cuspidatum</i>		<i>Oxycoccus quadripetalus</i>
	<i>S. papillosum</i>		<i>Vaccinium myrtillus</i>
	<i>S. tenellum</i>		<i>Rhynchospora alba</i>
	<i>S. pulchrum</i>		<i>Narthecium ossifragum</i>
	<i>S. plumulosum</i>		<i>Drosera rotundifolia</i>
	<i>Calluna vulgaris</i>		<i>Cladonia sylvatica</i>
	<i>Erica tetralix</i>		<i>C. uncialis</i>
	<i>Eriophorum angustifolium</i>		<i>Aulacomnium palustre</i>
	<i>E. vaginatum</i>		<i>Hypnum cupressiforme</i>
	<i>Molinia caerulea</i>		<i>H. schreberi</i>
	<i>Scirpus caespitosus</i>		<i>Rhacomitrium lanuginosum</i>
	<i>Empetrum nigrum</i>		<i>Polytrichum strictum</i>
	<i>Andromeda polifolia</i>		

(although present, *Scirpus* is omitted from Fig. 10)

Scattered in the Regeneration Complex one can find conspicuous tufts of vegetation which we named "*Eriophorum* islands". They are formed by an unusually tall and dense growth of *Eriophorum vaginatum*, from 0.5 to 3 m. in diameter. *Scirpus caespitosus*, *Erica*, *Andromeda* and *Oxycoccus quadripetalus* are frequently present, and very often part of the raised mound is formed of

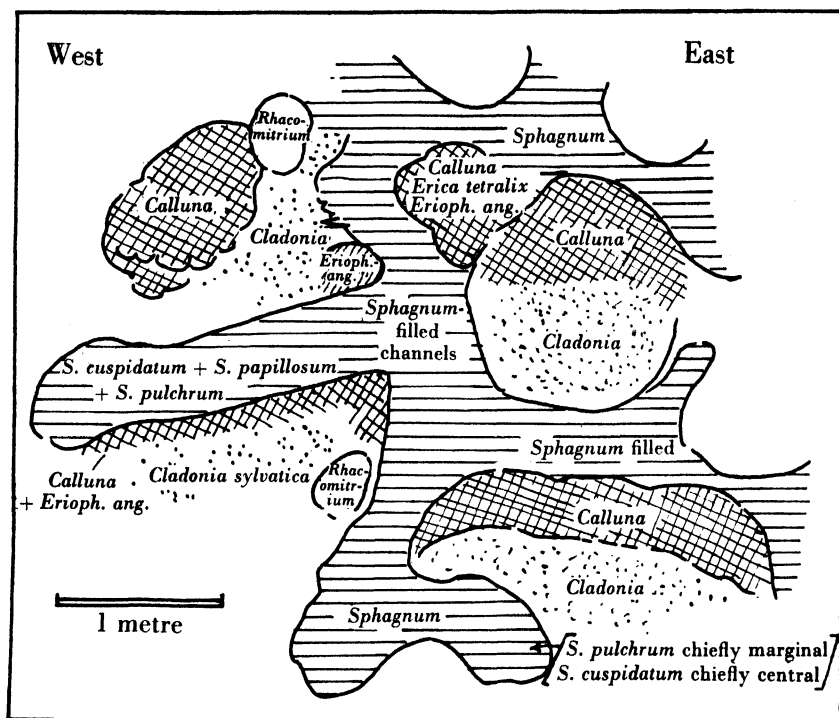


FIG. 8. Sketch of filling-up Regeneration Complex. This shows some differences from the "normal" structure of Regeneration Complex. The hummocks are all old and not building up: there are few living *Sphagnum* hummocks but all the channels are tending to fill up with *Sphagnum* cushions. The old hummocks tend to have *Calluna* on the windward side and *Cladonia* on the other: they also carry *Eriophorum vaginatum*, *Rhacomitrium* and a little *Scirpus*. *Drosera intermedia* and *Rhyncospora alba* come in at the *Sphagnum cuspidatum* stage, but *Narthecium* somewhat later.

a "moss cushion" of *Leucobryum*, *Sphagnum plumulosum*, or *Sphagnum rubellum*. There are also several species associated with these islands or mounds which are rare in the main Regeneration Complex vegetation, and made them seem worth special attention. They are:

<i>Empetrum nigrum</i>	f.	<i>Hypnum schreberi</i>	o.
<i>Vaccinium myrtillus</i>	o.	<i>Polytrichum commune</i>	o.
<i>Aspidium spinulosum</i>	o.	<i>P. strictum</i>	f.
<i>Aulacomnium palustre</i>	f.		

That part of the *Sphagnetum* which is not included in the Regeneration Complex may be designated "marginal *Sphagnetum*" and is indicated on the

map of Fig. 4 by fine-grained stippling. It extends as an encircling zone all round the bog at the upper edge of the rand, though on some radii it is more poorly developed than elsewhere; thus it is most well marked and most nearly approaches the Regeneration Complex type in the area to the south-east of the Scirpetum. The vegetation shows its essential resemblance to the Regeneration Complex in the vitality of *Sphagnum*, and the occurrence of similar pools and corresponding stages in consolidation. The species list is largely similar and *Eriophorum* islands occur here also, but there are certain features of the Regeneration Complex which are lacking.

(1) *Sphagnum pulchrum* is absent, so that the stage in colonization following *S. cuspidatum* is occupied solely by *S. papillosum*.

(2) The Regeneration Complex is carried by a markedly quaking ground surface. In the rest of the Sphagnetum the ground is more stable though it can still be made to quake by jumping on it. This is true for all parts of the bog.

(3) *Rhynchospora fusca* is found only in one or two completely isolated patches.

(4) *Drosera longifolia* and *D. intermedia* are infrequent.

(5) *Scirpus caespitosus* is a rather more conspicuous component of the vegetation.

In general it may be said that the typical regeneration cycle is obscured, possibly because suitable ecological conditions for typical development hold good over such a narrow zone that most of the Sphagnetum is in a transitional state to the types of community on either side of it. Fig. 9 shows a 5 m. quadrat taken in this region. It has a general resemblance to the quadrat of Fig. 7, and differs chiefly in the absence of *Sphagnum pulchrum*.

E. *Scirpetum*

The Scirpetum differs from the Sphagnetum in the relative unimportance of *Sphagna* and the dominance of the whole area by one species, *Scirpus caespitosus*¹. A species list is very similar for the two communities, but the structure of the vegetation is very different. In the Scirpetum, pools which are more than about 30 cm. across are rare, and where they occur are usually quite filled with *Sphagnum cuspidatum*. *S. papillosum* is present in small amount but not forming conspicuous patches. The *Scirpus* forms low tough tussocks up to 60 cm. in diameter but not usually over 15 cm. in height, and the tussocks are close enough together to give a sward-like appearance to the vegetation. *Calluna*, though present, is not so abundant or luxuriant as to break the impression of an even surface. *Eriophorum vaginatum* and *Erica tetralix* are frequent, and *Narthecium ossifragum* common, while *Cladonia sylvatica* is occasional to frequent, but occurs in very small patches.

¹ The plant present on Tregaron bog may in all probability be referred to *Scirpus austriacus*, one of the two species into which *S. caespitosus* is now divided.

A very marked characteristic of the association is the abundance of *Sphagnum tenellum*. This is a small shade-loving species which is quite inconspicuous at a first glance, but may readily be found throughout the *Scirpetum*, occupying the peat surfaces between the *Scirpus* shoots and lining the sides and often the bottoms of the narrow clefts and small pools which are left between the *Scirpus* tussocks.

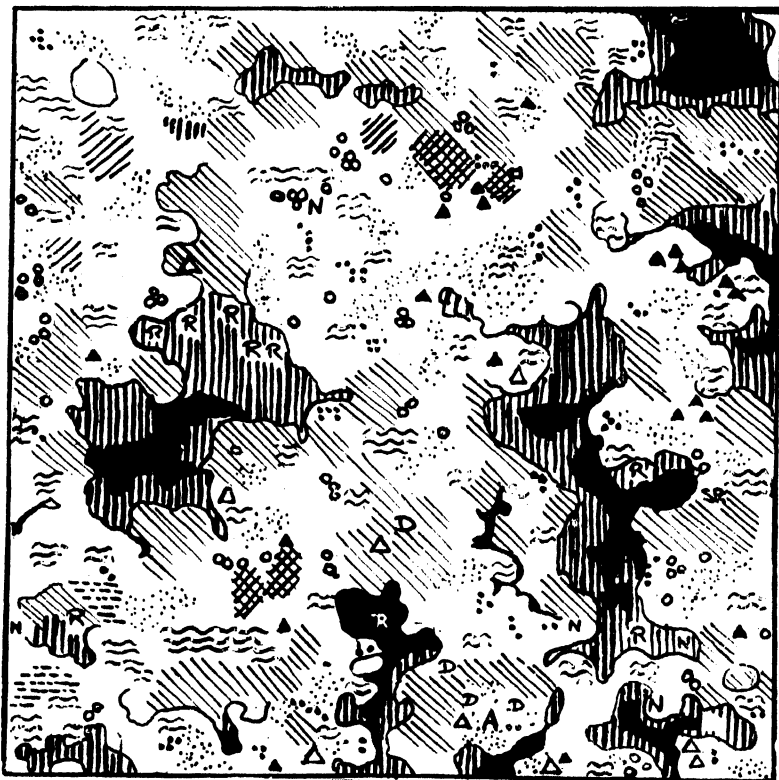


FIG. 9. 5 m. quadrat showing *Sphagnetum* from the south-eastern region of the bog. (Quadrat 2, position J, 120.)

These clefts contain an almost constant selection of Bryophyta, namely:

Sphagnum cuspidatum
S. tenellum

Lepidozia setacea
Diplophyllum albicans

The levelled transects shown in Fig. 6, *a*, *b* give the type of profile obtained in this association, and contrast with the corresponding data for the Regeneration Complex in the narrow steep-sided hollows and the rarity of large open pools. The quadrat given in Fig. 10 shows these features and also the abundance of *Sphagnum tenellum*. *Scirpus* was so abundant that it was not mapped in making this quadrat, but may be assumed to be growing everywhere except where mud or *Sphagnum cuspidatum* are indicated.

The nature of this association precludes the idea that it shows any cyclic behaviour, so that if peat is being formed here at present, it must be made mainly by *Scirpus* and to a small extent by *Sphagnum cuspidatum*. Nevertheless it is important to note that the *Scirpus* tussocks are based on a peat which is clearly sphagnaceous and resembles that underlying the Sphagnetum.

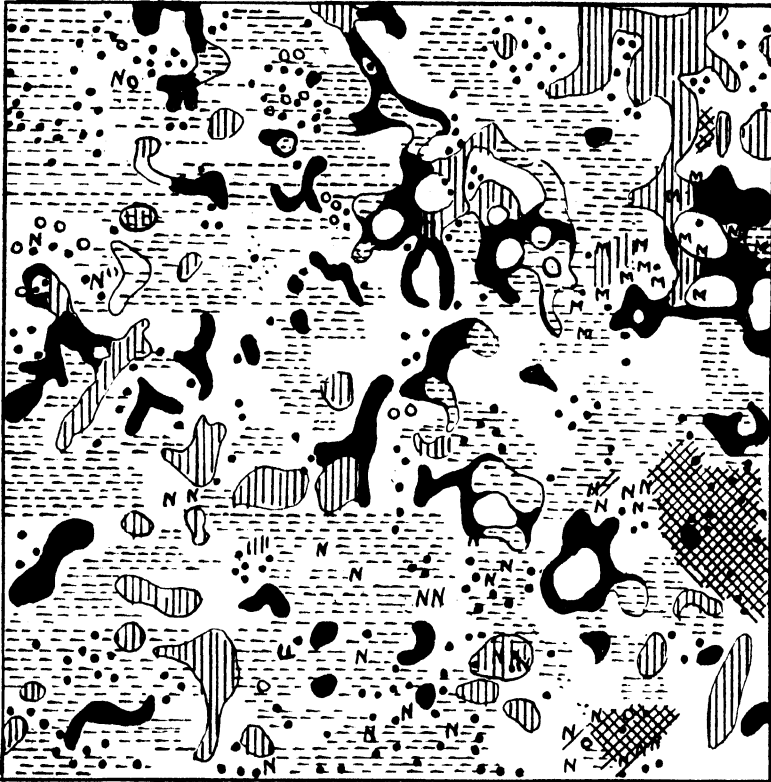


FIG. 10. 5 m. quadrat in Scirpetum, *Scirpus* was so abundant that it was not recorded. It can be taken as generally distributed throughout. (Quadrat 4 position I, 200.)

There is a fairly sudden transition between the Scirpetum and the Molinietum which lies towards the bog centre, but on the outer margin of the Scirpetum there is a long and gradual change into the surrounding Sphagnetum.

The salient points indicating the transition have been extracted from the 5 m. quadrats and reproduced in the form of diagrams given in Figs. 11 and 12. Quadrats 1, 2 and 4 have already been figured in full to illustrate Regeneration Complex, marginal Sphagnetum and Scirpetum respectively; quadrat 3 was taken in the transition region on the south-east border of the Scirpetum.

Fig. 11 shows the diminution in pool area, or rather, the altered distribution of heights and hollows in passing from the Sphagnetum types to Scirpetum,

together with the progressive diminution in *Sphagnum papillosum* and *Cladonia sylvatica*. Fig. 12 shows the converse increase of *Sphagnum tenellum* and, to a less extent, of *Erica tetralix*, while *Calluna* has diminished markedly in frequency.

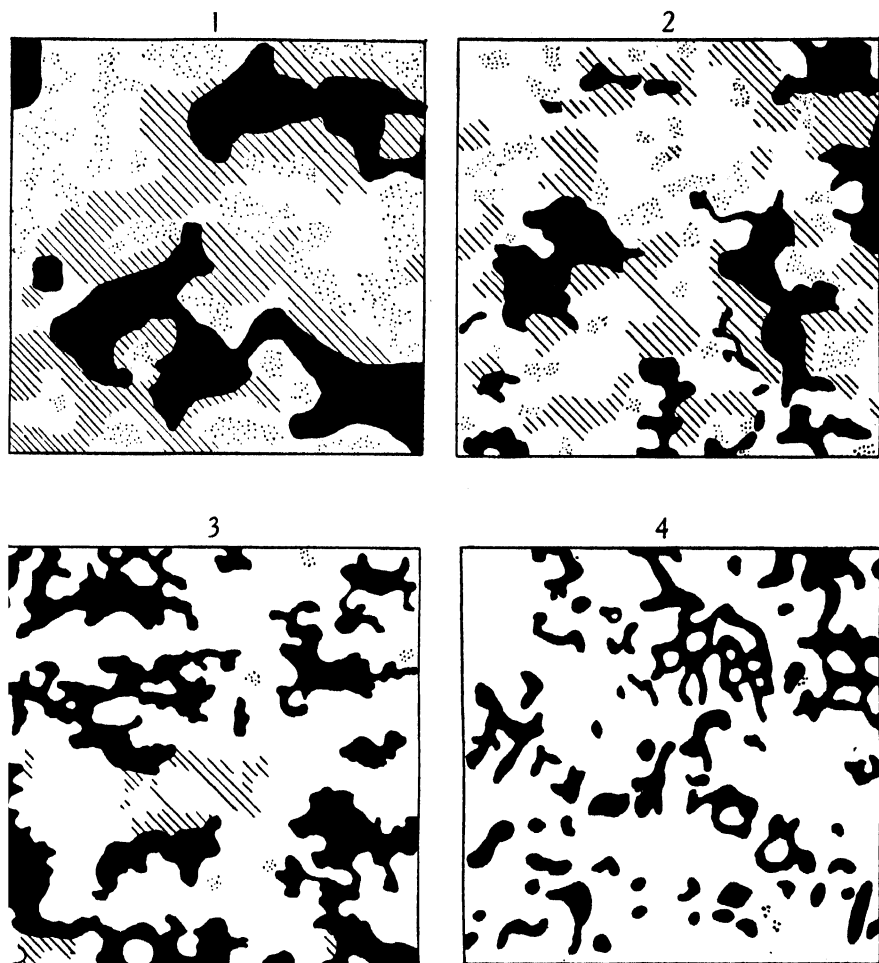


FIG. 11. Analysis of four quadrats from Regeneration Complex (quadrat 1), Sphagnetum (quadrat 2), Sphagnetum Scirpetum transition (quadrat 3) and Scirpetum (quadrat 4). Black, pools with open water; diagonal shading, *S. papillosum*; stipple, *Cladonia sylvatica*.

The "islands" which were described for the Sphagnetum appear also in the Scirpetum but show here more variety and a greater significance in their distribution.

In the first place two main types are present: *Eriophorum* islands and *Molinia* islands. The former resemble those already described in having large *Eriophorum* tufts, but many of them show a well-marked centric structure with the *Eriophorum* in the centre, somewhat raised, surrounded by a zone of

Eriophorum mixed with tall *Scirpus* with *Calluna*, *Erica tetralix*, *Narthecium*, *Empetrum*, and *Hypnum schreberi*. Fig. 13 shows a transect made across one such island.

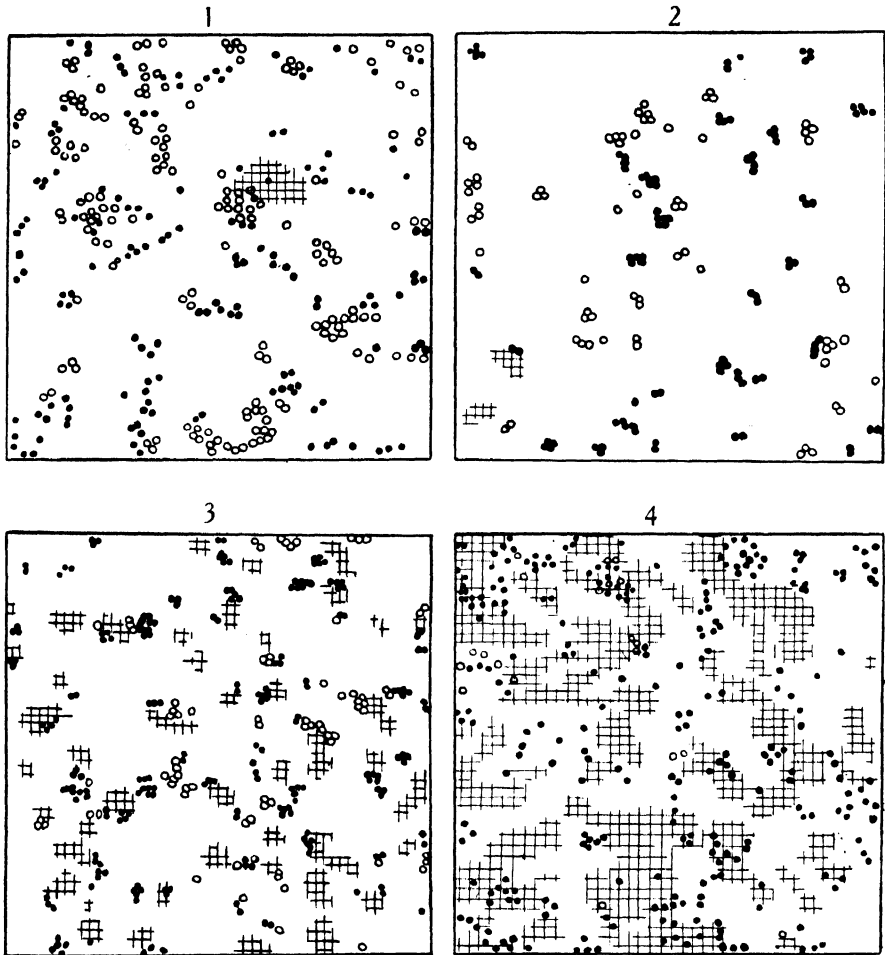


FIG. 12. Same four quadrats as in Fig. 11. Black circles, *Erica tetralix*; open circles, *Calluna vulgaris*; shading, *Sphagnum tenellum*.

The *Molinia* islands also contain tall *Eriophorum vaginatum* but bear *Molinia* tussocks whose bright green causes these islands to be a conspicuous feature in the general drab colour of the *Scirpetum*. They do not often show a centric structure and differ somewhat in the species which are characteristically associated. These are:

<i>Potentilla erecta</i>	f.	<i>Holcus lanatus</i>	o.
<i>Rumex acetosa</i>	o.	<i>Aspidium spinulosum</i>	v.f.
<i>Juncus effusus</i>	o.	<i>Osmunda regalis</i>	f.
<i>Luzula multiflora</i>	o.	<i>Dicranium scoparium</i>	o.
<i>Anthoxanthum odoratum</i>	o.	<i>Polytrichum commune</i>	v.f.
<i>Deschampsia caespitosa</i>	o.		

The following species occur, but are much less frequent than in the *Eriophorum* islands:

Oxycoccus quadripetalus
Andromeda polifolia
Erica tetralix
Eriophorum angustifolium

Polytrichum strictum
Sphagnum papillosum
S. rubellum

There is no evidence that *Molinia* invades an already formed *Eriophorum* island, thus converting it to a *Molinia* island: the tussocks of the two species grow side by side and appear to develop contemporaneously. The islands were

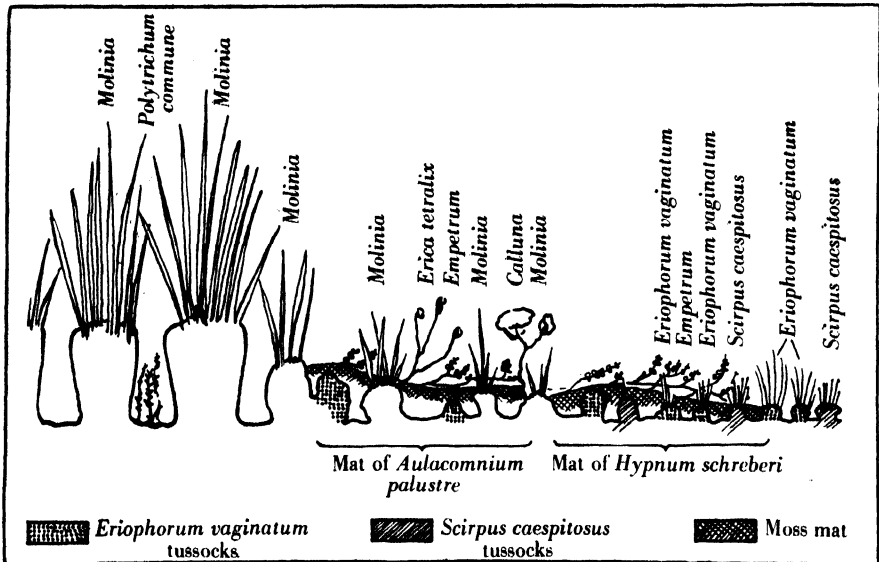


FIG. 13. Line transect across a *Molinia* "island".

mapped along a belt transect 20 m. wide crossing the bog along line I of the grid system, thus passing through marginal *Sphagnetum* at either end, and *Scirpetum* and *Molinietum* more centrally. It will be seen from Fig. 14 that the *Molinia* islands increase in frequency in that part of the *Scirpetum* which borders on the *Molinietum*. It is of interest that a similar investigation of a parallel belt lying farther to the south (line L) showed that no *Molinia* islands occurred in it, but that there was a change in the relative abundance of the species associated with the *Eriophorum* islands, parallel to that accompanying the change from one type of island to the other along line I. For example, *Polytrichum commune* became more frequent than *P. strictum*, *Aspidium spinulosum* increased and *Sphagnum rubellum* decreased in frequency.

Broadly speaking, it seems as though the appearance of *Molinia* in the islands is the last and most conspicuous symptom of a change in habitat conditions in passing from the margin of the bog towards the centre, a change which is expressed to begin with by the altered abundance of the less con-

spicuous species. Thus more marginally there are the simpler *Eriophorum* islands associated commonly with moss mounds and varying considerably in associated species: somewhat more centrally occur the "centric" *Eriophorum* islands (mainly in the Scirpetum) with *Scirpus* rather more important, and *Narthecium* as a characteristic associate. *Polytrichum commune* and *Aspidium spinulosum* increase in frequency at this stage. Thirdly in the most central part of the Scirpetum, *Molinia* becomes a constant component of the islands.

It is perhaps reasonable to see the final step in this zonation exhibited in the fusion of *Molinia* islands into an independent association described here as the Molinietum.

F. Molinietum

The area occupied by this association is not very extensive, as Fig. 4 indicates, but it lies nearest the centre point of the bog, though not at the summit of it. *Molinia* is the dominant species, but *Betula pubescens* is very frequent, and as many of the trees are still quite young it may be that this species will ultimately attain dominance. Some of the trees, however, appear well grown, having trunks up to 10 or 15 cm. in diameter. *Sphagna* are rare and their place seems to be taken by other bryophytes such as *Aulacomnium palustre* and *Hypnum cupressiforme*. The list given below is not exhaustive but includes all the main components of the association:

Empetrum nigrum
Vaccinium myrtillus
V. oxycoccus
Andromeda polifolia
Erica tetralix
Calluna vulgaris
Betula pubescens
Scirpus caespitosus

a.
 o.-f.
 f.
 o
 f.
 a.
 a.
 o.-f.

Eriophorum angustifolium
Molinia coerulea
Sphagnum plumulosum
S. tenellum
Aulacomnium palustre
Hypnum cupressiforme
H. schreberi

o.-f.
 d.
 o.
 r.-o.
 o.-f.
 f.
 o.

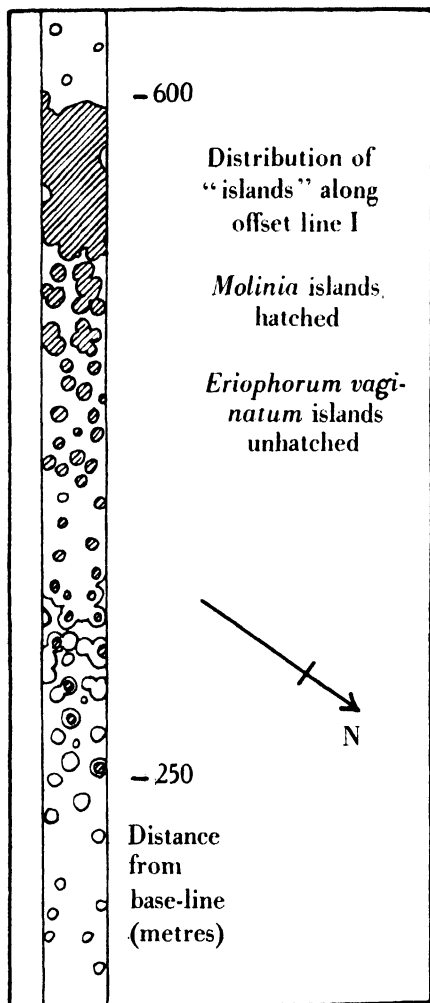


FIG. 14. Rough belt transect along line 8 of the grid, to show the distribution of "islands".

Just as in the case of the *Scirpetum*, an investigation of the subsoil of the *Molinietum* shows typical *Sphagnum* peat, and though the surface vegetation forms a resistant mat, the ground as a whole quakes considerably. The vegetation is illustrated by the 5 m. quadrat shown in Fig. 15.

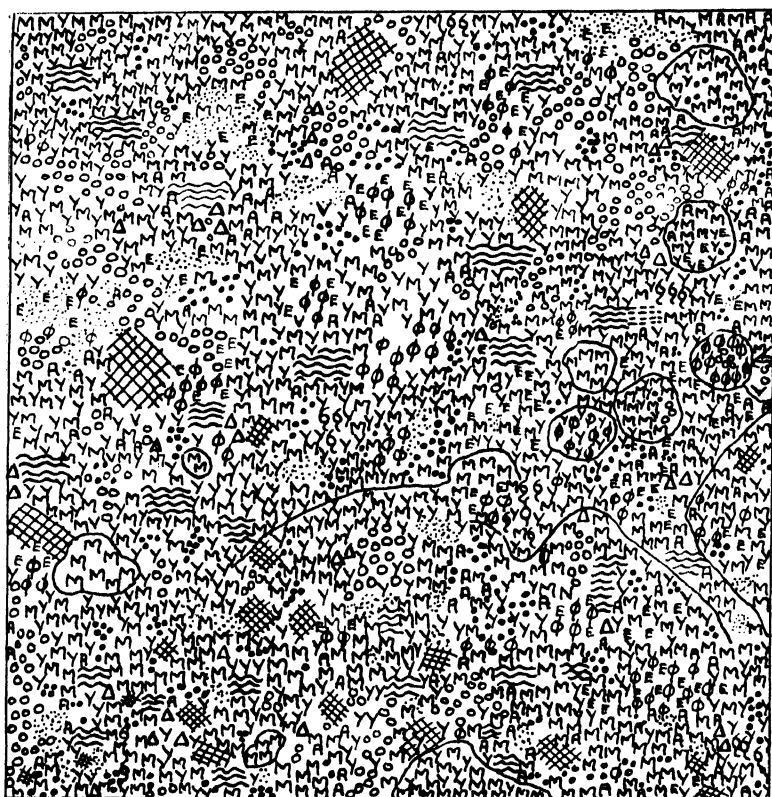


FIG. 15. 5 m. quadrat in *Molinietum*. (Quadrat 8, position K, 380.)

On the eastern and southern sides the change from *Scirpetum* to *Molinietum* is abrupt, but on the north-western side there are indications of a gradual transition between the *Molinietum* and the adjacent Regeneration Complex. Two quadrats were mapped in the intermediate region, making a series of four with the quadrats given in Figs. 9 and 15. Certain data have been extracted from this series and presented in Fig. 16. Here are shown the gradual filling up of pools, and the entrance of *Molinia* and *Empetrum* as the *Molinietum* is approached. There is a quite definite region which shows a marked abundance of *Eriophorum angustifolium*, characteristically a colonist of drying pools, and this is represented in the second quadrat of the series. Whether or not this series of quadrats represents a real succession from Regeneration Complex to *Molinietum* the evidence does not seem sufficient to

decide, but even though the *Eriophorum angustifolium* does not represent a successional stage, it is so obvious a feature that it must have some ecological significance, which will be made clear by increased knowledge of this and other bogs.

G. *Callunetum*

A rather ill-defined area to the north-east of the bog bears a vegetation dominated by *Calluna vulgaris*. The character of the ground is conspicuous in being very rough and broken, for drainage channels are numerous and deep. The area lies on a sloping region which is drained away to the lower ground on the north, and it has been extensively encroached upon by peat cutting; some of the drainage channels leading towards the peat margin seem to be man-made. In many places the broken character of the surface is accentuated by the trampling of cows. A larger proportion of bare peat is exposed in this association than in any of the others described, and this is related to the erosion which seems to be a pronounced feature here.

The more rapid drainage implied by the character of the ground is possibly responsible for the luxuriant growth of the *Calluna*, which attains a greater height here than in the other associations, and gives this one its characteristic facies. Besides the *Calluna*, *Cladonia sylvatica* is a very conspicuous component of the vegetation. *Sphagna* are common and may colonize the channels, forming a tussock-like growth in places; species of the section *sub-secunda* are commoner here than in other parts of the bog. Pools occur here and there, sometimes containing *Sphagna*, more often bare save for *Rhynchospora alba*. Many of them link up into irregular drainage systems which tend to become filled up by a vigorous growth of *Eriophorum angustifolium*. *Scirpus* is abundant, both mixed with the *Calluna* and colonizing old channels, while *Molinia* occurs in sporadic patches.

It has been mentioned previously that the upper rand zone frequently shows vigorous growth of *Calluna* and *Cladonia*, and it seems probable that the *Callunetum* here described is a much extended and exaggerated example of this rand type. If the contour map of Fig. 3 is examined it can be seen that the marginal contours splay out at this north-eastern end of the bog in just such a way as might lead to the development of a larger area of what is essentially a rand type of vegetation. Topography and plant cover alike show that this community corresponds with the so-called "Still-Stand complex" of Osvald, in which the increased drainage conditions so much slow down peat formation that this barely keeps pace with the erosion and breakdown of bare peat surfaces. This heather-moor community corresponds more or less to the end stage of raised bog development envisaged by the ecologists who think that with increased height the bog growth gradually slows down and ceases.

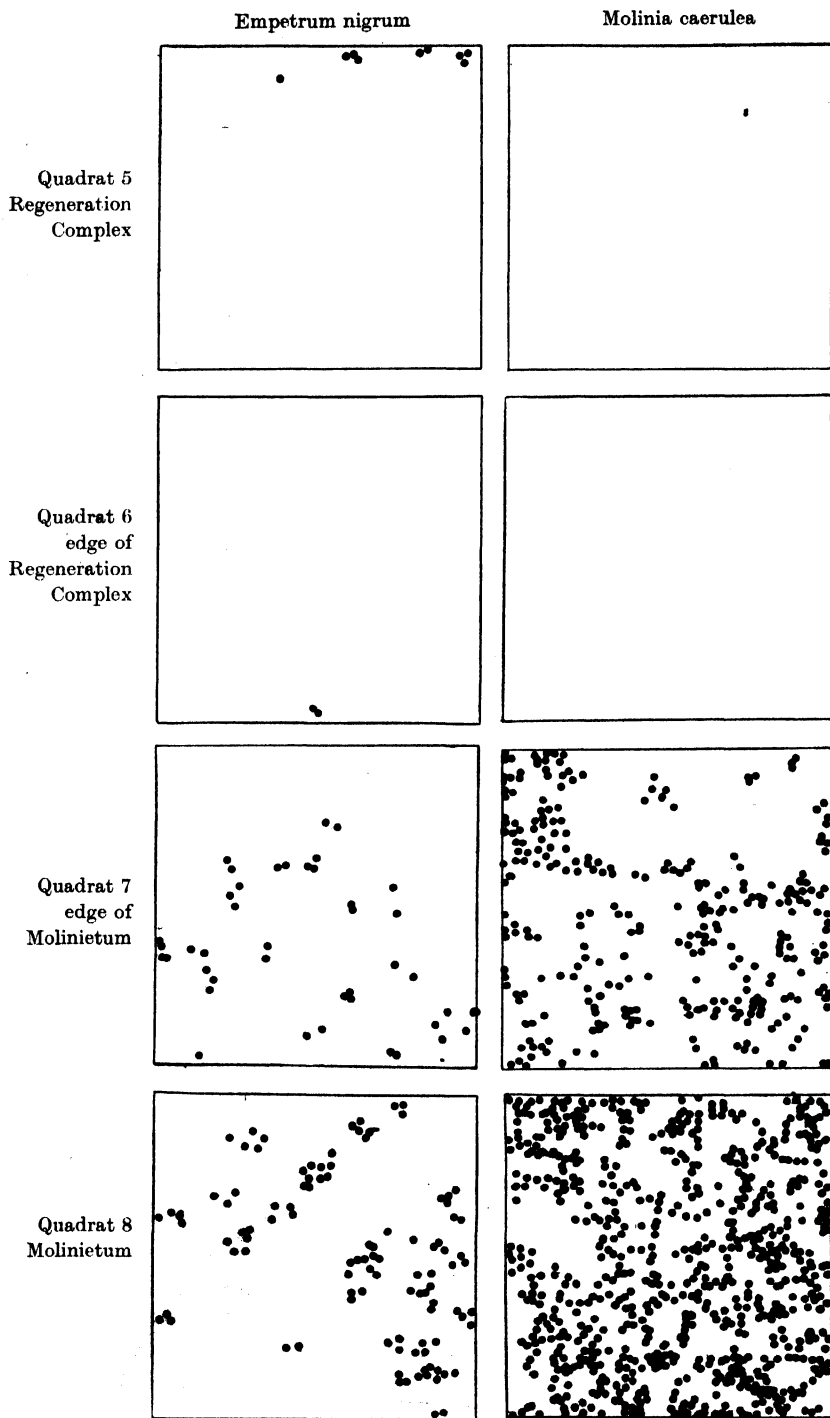
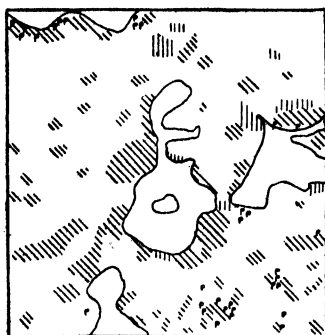
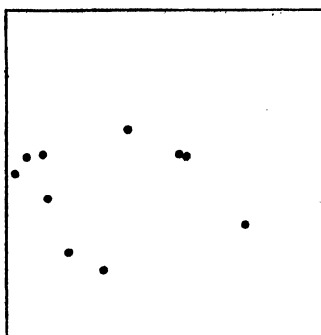


FIG. 16. Analysis of four quadrats showing gradation in characteristics from Regeneration Complex to Molinietum. In the third vertical column (pools and *Sphagna*)—vertical shading, *Sphagnum cuspidatum*; diagonal shading, *S. papillosum*; PPP, *S. pulchrum*.

Pools and Sphagna



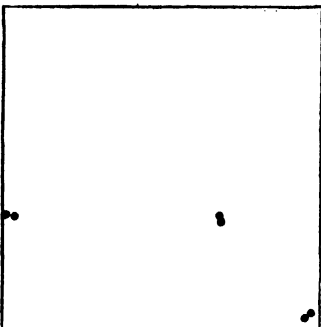
Eriophorum angustifolium



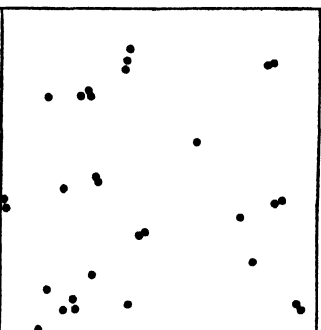
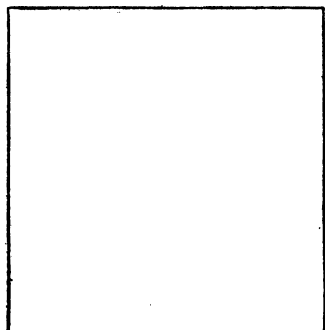
Quadrat 5
Regeneration
Complex



Quadrat 6
edge of
Regeneration
Complex



Quadrat 7
edge of
Molinietum



Quadrat 8
Molinietum

FIG. 16 (continued).

VI. SPATIAL DISTRIBUTION OF THE MAIN COMMUNITIES

The map given in Fig. 4 was derived from the information afforded by transects made along the transverse lines of the "grid" which was set up for this purpose. The grid consisted of a base-line roughly parallel to the river, with offsets *A*, *B*, *C*, etc., set out perpendicular to it every 100 m. Every 100 m. along each offset was marked off by a flag. Observations were made along the length of each offset from the edge of the river terrace at the east end to the peat cutting margin of the bog at the west end. One or two observers dealt with each of the offsets, and confined their attention to a belt of 20 m. in width, as nearly as they could estimate. The observer was instructed to walk along the offset until it was evident that a region had been reached in which the vegetation was different in character from that in the spot from which he started. He had then to retrace his steps to the point where he judged the transition between the two types to lie, and then work over the first part carefully, filling in the required information on a standardized card. He would deal in this way with each section of the transect which appeared to be homogeneous in character, until the far end of the transect was reached. Sometimes, especially near the bog margins, the changes in plant cover would be frequent, giving short sections of 20–50 m. to be described, while in the central part of the bog one description would hold good over lengths of 150–200 m.

The estimations which observers were required to make fell into three categories.

(a) Estimation of the percentage of the whole area covered by the following components:

Pools more than 30 cm. wide.

Pools less than 30 cm. wide.

Living *Sphagnum* carpet (excluding pool *Sphagna* and *S. tenellum* which is not a peat builder).

Scirpus and *Eriophorum vaginatum*.

Cladonia sylvatica.

These had to add up to 100%. In addition an estimation was made of the percentage of the area covered by *Calluna*. This allowed for the fact that *Calluna* does not form part of the field layer.

(b) Division of the area covered by pools into percentages of the major pool types, viz.:

Pools filled with *Sphagnum* spp.

Pools partly filled with *Sphagnum* spp.

Pools carrying sparse growth of *Rhynchospora alba*.

Pools carrying dense growth of *Rhynchospora alba*.

Pools bare or with *Zygogonium ericetorum* only.

(c) Estimation of frequencies of phanerogams on a scale of 0–5, of cryptogams on a scale of 0–3, and various other features such as slope, roughness of

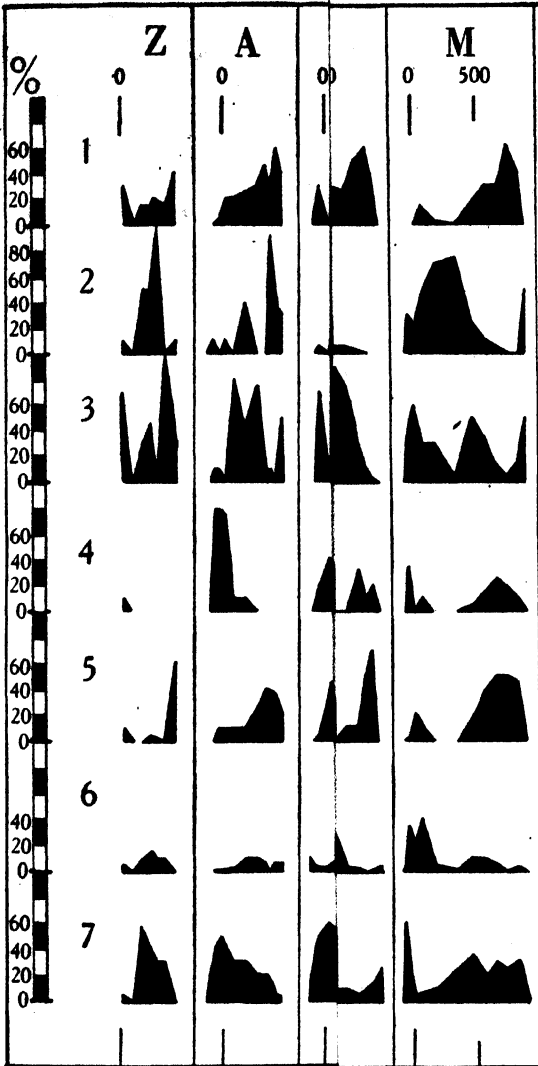


Fig. 17. Results of quantitative estimate of surface covered by pools more of the area covered by pools, with of surface covered by *Calluna*.

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 |ependent observers, but other
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 ve were more successful than
 s involved in the method. The
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 y limited in their distribution.
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 ies such as *Sphagnum tenellum*
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 ined, in order to illustrate the
 resting results. The estimated
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 the resulting small graphs are
 bits the behaviour of different
 l row exhibits the variation of
 he bog.

area of the total surface which
h. It can be seen that there is
c in the central region of each
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those regions which show low
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the distribution of pool types
ere pools are altogether scarce,
lues of 80–100% in the graphs
bare ground is very rare in this
building up the surface to form

a partial filling of *Sphagnum* is the area just discussed, and is gives for total area of pools. The types treated in the third and most southern parts of the bog,

VI. SPATIAL DISTRIBUTION

The map given in Fig. 4 was made from transects made along the transverse offsets for this purpose. The grid consisted of 100 m. offsets, set out with offsets A, B, C, etc., set out 100 m. along each offset was marked along the length of each offset from the end to the peat cutting margin of the bog. Servers dealt with each of the offsets 20 m. in width, as nearly as they could, to walk along the offset until it was clear which the vegetation was different from which he started. He had then to mark the transition between the two types of vegetation carefully, filling in the required information in this way with each section of the bog homogeneous in character, until the far end of the bog, especially near the bog margins, the giving short sections of 20-50 m. the bog one description would hold.

The estimations which observations gave were in the following categories.

(a) Estimation of the percentage of the area covered by the following components:

Pools more than 30 cm. wide.

Pools less than 30 cm. wide.

Living *Sphagnum* carpet (excluding areas where it is not a peat builder).

Scirpus and *Eriophorum vaginatum* carpet.
Cladonia sylvatica.

These had to add up to 100% of the area covered by the vegetation.

Calluna does not form part of the vegetation. The following rows show the following characteristics. (1) Percentage of the area covered by the vegetation.

(b) Division of the area covered by pools partly filled with *Sphagnum*. (4) That percentage of the area covered by pools partly filled with *Sphagnum* (excluding *S. cuspidatum* and *S. tenellum*). (7) Percentage of the area covered by pools partly filled with *Sphagnum*.

Pools filled with *Sphagnum* spp.

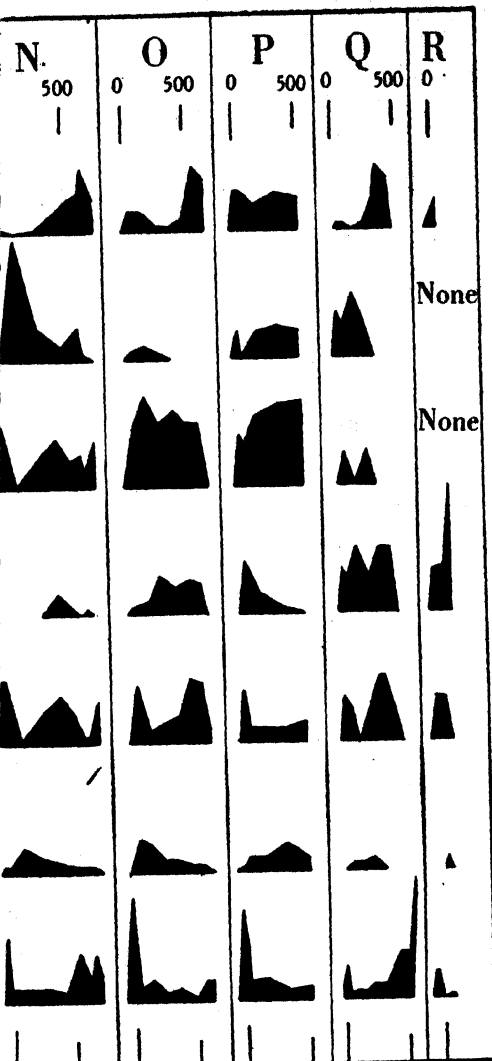
Pools partly filled with *Sphagnum*.

Pools carrying sparse growth of *Sphagnum*.

Pools carrying dense growth of *Sphagnum*.

Pools bare or with *Zygonium*.

(c) Estimation of frequencies of vegetation types on a scale of 0-3, and various other characteristics.



ground, presence of drainage channels, etc., also on a scale of 1-3 according to interpretations that were agreed upon beforehand.

The value of the results obtained varied considerably according to the particular quantity estimated. In some cases there seemed a remarkable consistency between the data given by the independent observers, but other determinations were evidently badly chosen, for the results were of little significance when considered for the bog surface as a whole. Fortunately, the percentage estimations under (a) and (b) above were more successful than could have been foreseen, considering the errors involved in the method. The frequency estimations were very useful for species such as *Molinia* and *Sphagnum pulchrum* which are fairly definitely limited in their distribution. This transect method made it possible to establish the actual positions of these limits. The failures were concerned in the first place with species such as *Erica tetralix*, which occur all over the bog but are never dominant and never really rare, and secondly with small species such as *Sphagnum tenellum* and *Oxycoccus* which cannot be recognized when the observer is standing up.

Fig. 17 gives a selection of the data obtained, in order to illustrate the method and to show some of the more interesting results. The estimated magnitudes are plotted against the position along each transect, starting on the left with the eastern end of the transect; the resulting small graphs are arranged together so that a vertical row exhibits the behaviour of different characters along one transect, and a horizontal row exhibits the variation of one character from the north to the south of the bog.

The top line of graphs gives the percentage area of the total surface which is covered by pools of more than 30 cm. width. It can be seen that there is a general tendency for lower values to occur in the central region of each transect, and that zero values have been recorded over considerable lengths in the part of the bog included by lines *H* to *L*. The estimations of the percentage area covered by pools of smaller size showed a high degree of personal error, but were never more than 3%. Hence those regions which show low percentages of pool area in Fig. 17 may be taken to be genuinely poor in pools.

The four rows of graphs next below show the distribution of pool types over the bog surface. It is apparent that where pools are altogether scarce, as in the centre of lines *I* and *J*, there are values of 80-100% in the graphs for pools filled with *Sphagnum*, indicating that bare ground is very rare in this region and that *Sphagnum* have built up or are building up the surface to form a uniform vegetation.

The maximum proportion of pools with a partial filling of *Sphagnum* is found in the regions immediately surrounding the area just discussed, and is usually associated with high values in the curves for total area of pools. The same can be said in general of the other two types treated in the third and fourth rows, and in the most northern and most southern parts of the bog,

covered by lines *A* to *D* and *M* to *P* respectively, these three types are not clearly differentiated. Lines *E* to *L*, however, show a well-marked zonation if one examines the shift in position along the transect in passing from the maximum value of one type to the maximum of the next. This is especially well shown on the western half of the bog. Thus on line *L*, there is a central maximum of pools filled with *Sphagnum* from about 200–500 m., followed by the peak values of part-filled *Sphagnum*, "*Zygogonium* only", and "sparse *Rhynchospora*", at about 550, 850 and 1000 m., respectively.

Generally speaking, the data on pools seem obscure at the northern end, included in lines *A* to *C*, and this is because the transects pass for the most part through the irregular vegetation of the *Callunetum*, and lie tangentially to the main concentric zonation of the bog, as may be seen from Fig. 4. A similar obscurity is involved in the result from lines *P*, *Q* and *R*; the two latter in fact have not been included in Fig. 17 because they were short and were concerned almost entirely with the lower rand vegetation or the regions disturbed by former peat cuttings.

The lowest row of graphs in Fig. 17 deals with the frequency of *Calluna*. The estimations were given as percentage of the total area covered by *Calluna*, irrespective of other vegetation that might be growing beneath it. As the figure shows, the general pitch of the estimations varies considerably from one observer to another, but in spite of this two main conclusions may be drawn. First, *Calluna* is much more abundant over the northern end of the bog as a whole, and secondly, it almost invariably shows a marked increase marginally. These figures give quantitative illustration of the presence of the *Callunetum* and of the *Calluna*-rich section of the rand, both already described.

The primary data exhibited in Fig. 17 can be used to give maps of the kind shown in Figs. 19–28, by selecting arbitrary values from the graphs in Fig. 17, values which seem to express the dividing line between frequency and rarity of a species or between high and low proportions of a quantitative variable. Fig. 20, for example, is derived from the data expressed in the fifth row of Fig. 17 by taking 15% as the dividing line. The regions along each transect, where values over 15% were recorded, are blacked in, and corresponding points on the different transects joined up so as to extrapolate the transect data to cover the whole bog surface.

Not all the primary data lend themselves to this treatment: it is almost impossible for instance to select a value for percentage cover of *Calluna* which does not give a map with a haphazard appearance quite at variance with the known facts of its frequency distribution.

There is much irregularity in outline of the figures due to individual variation between different investigators, but if the maps are taken to give the broad outline of distribution they do yield legitimate conclusions concerning the bog vegetation.

(i) *Channels*

In recording the presence of channels in a particular region of a transect, a note was made as to whether they were "eroding" or "overgrown" and the results so obtained are symbolized in Fig. 19. The former type referred to those channels which were steep-sided and showed a high proportion of bare peat, both on the sides and bottom, and gave the impression of carrying a flow of water which might at times be fast enough to undercut the vegetation bordering the channel. "Overgrown" channels, on the other hand, showed vigorous colonization by various plants, often *Sphagna*, especially *S. cuspidatum*, but frequently also *Scirpus*, *Eriophorum* spp. and *Molinia*. Occasionally near the outer margin of the bog *Juncus communis* (? *effusus*) was found as a colonist.

Fig. 19 shows that the "overgrown" type is much less frequently recorded on the western margin of the bog; the reason is that such channels are more characteristic of the lower parts of the rand which are just those which, on the west of the bog, have been destroyed by peat cutting.

The presence of channels in an area is taken as a diagnostic character of the rand vegetation, and the eroded channels indicate the "upper rand" zone.

Fig. 29 gives a more detailed picture of the characteristics of a single rand drainage channel from its origin on the outer edge of the Sphagnetum by the linkage of shallow pools, through the central stage of deep erosion through the rand, to the final dispersion and disappearance in the Molinietum at the foot of the rand above the river terrace. The mean slope of the stream bed is somewhat less than 1° , and not until this slope is approached at the bog margin do the pools link together to form a stream. The tributary shown entering the stream at E 0 is now blocked and partly overgrown by *Sphagnum cuspidatum*, *Rhynchospora alba* and tussocks of *Sphagnum papillosum*, *Eriophorum angustifolium* and *Molinia*.

(ii) *Pools with "sparse Rhynchospora"*

Pools of this type are often large, that is, up to 2 m. across, and flat-bottomed, with firm black peat in which occurs a sprinkling of the annual *Rhynchospora alba*. The plants are on an average 10 cm. apart and do not form a green carpet of vegetation, while *Sphagnum cuspidatum* is absent or very rare. Very frequently the pools are linked together, especially in the direction radial to the bog as a whole, so that after heavy rainfall the water can be observed to flow off from one to another fairly rapidly. The distribution map in Fig. 20 shows that the zone of abundance of this type covers that which includes drainage channels, but also extends internally to the latter. It lies, therefore, where the slope of the bog surface is beginning to increase rapidly so that these linked pools form part of the surface drainage system. It seems

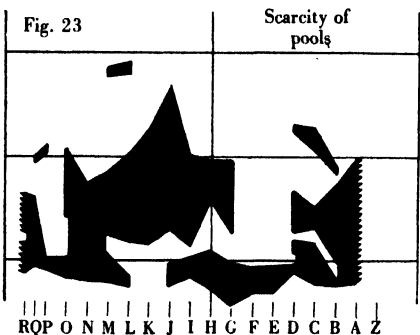
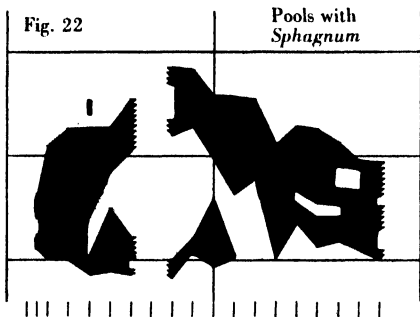
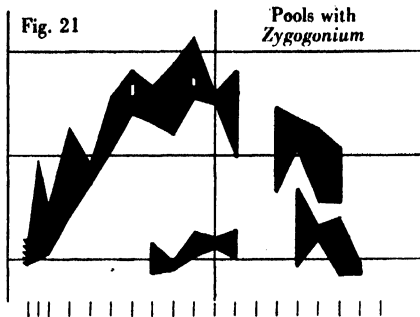
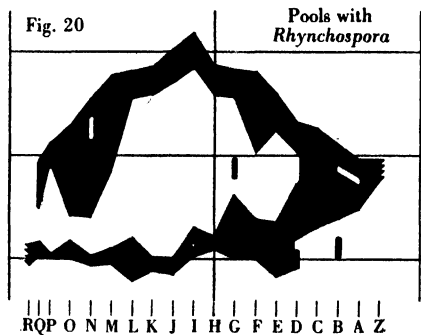
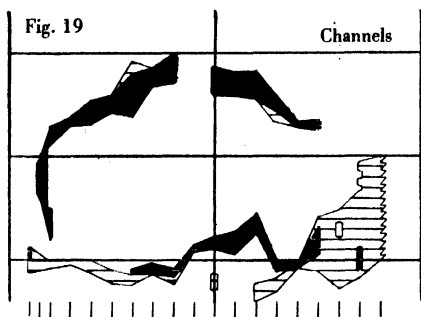
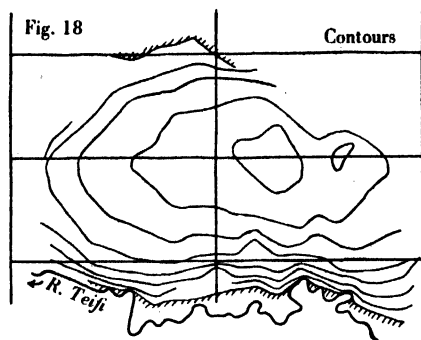


FIG. 18. Contour map of the bog.

FIGS. 19–28. Results of estimations made along the transects of the grid, expressed in the form of distribution maps. Saw-edging indicates that estimations were not made on the adjacent transect.

FIG. 19. Black indicates presence of eroding channels, shading the presence of overgrown channels.

FIG. 20. Area in which 15% or more of the area covered by pools consists of pools with sparse *Rhynchospora*.

FIG. 21. Area in which 15% or more of the area covered by pools consists of pools with *Zygogonium* only.

FIG. 22. Area in which 20% or more of the area covered by pools consists of pools partly filled with *Sphagnum*.

FIG. 23. Areas in which less than 15% of the surface is covered by pools more than 30 cm. wide.

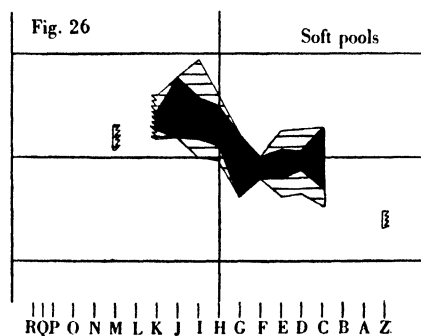
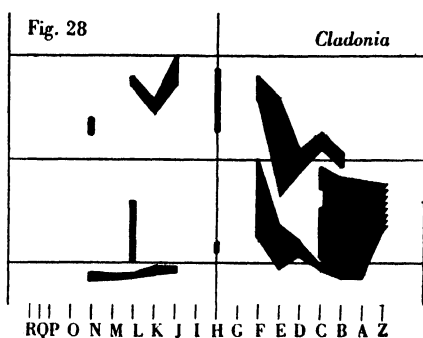
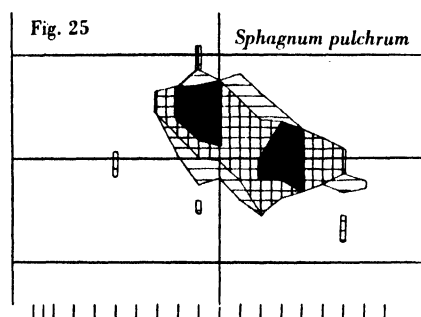
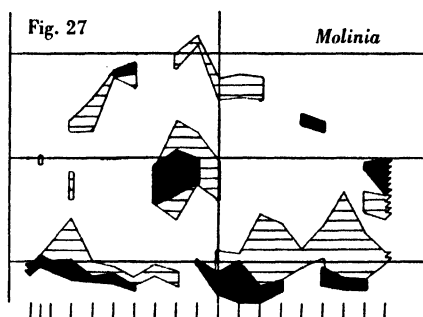
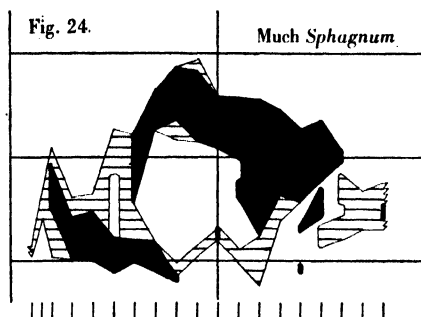


FIG. 24. Black, areas with 15% or more of the surface covered by living *Sphagnum*; shaded, the corresponding areas 10–15%.

FIG. 25. Black, *S. pulchrum*, has frequency 3; cross-hatch, frequency 2; single hatch, frequency 1.

FIG. 26. Black, all the pools "soft"; shading, some of the pools soft.

FIG. 27. Black, *Molinia* has frequency 4 or 5; shaded, frequency 1, 2 or 3.

FIG. 28. *Cladonia* covers 15% or more of the surface.

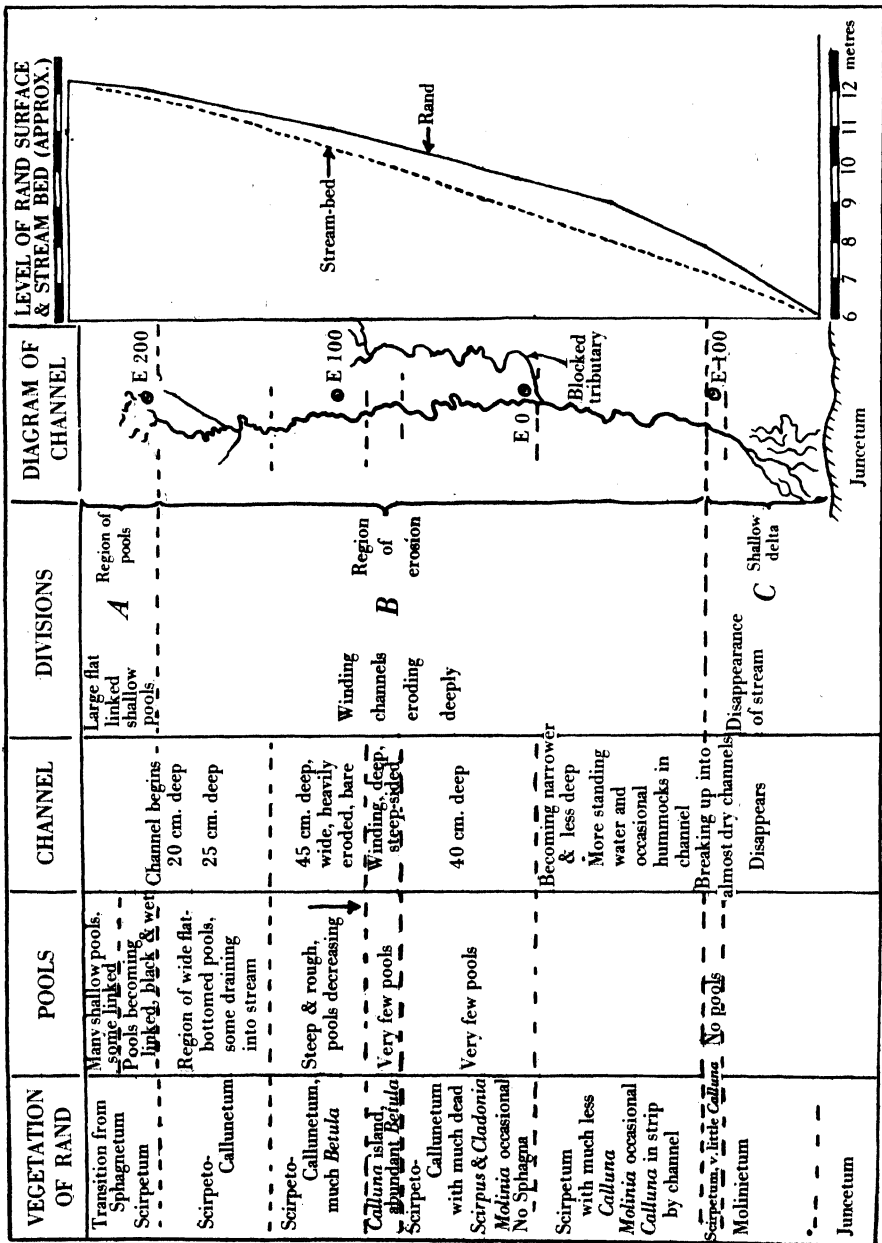


FIG. 29. Detailed investigation of a single drainage channel of the rand, lying near offset E.

likely that on this account they are unsuitable for colonization of *Sphagna*, so that they show no tendency towards filling up and remain as bare and rather steep-sided pans.

(iii) *Pools with "Zygogonium only"*

These pools are very similar in character to those just described, but do not bear the abundance of *Rhynchospora*. They are also linked, and almost free from *Sphagna*, and, as Fig. 21 shows, are most abundant in a region almost coextensive with that indicated in Fig. 20. It is, however, slightly internal, a fact shown more clearly in Fig. 17. This means that they lie on a more gradual slope, so that drainage would tend to be slower, and standing water more frequent. It may tentatively be suggested that *Rhynchospora* cannot germinate or reach maturity if too often submerged, and so tends to be less abundant in the more central, and less sloping, regions of the bog.

A feature seen commonly in this, and occasionally in the foregoing, type of pool, is the breakdown of the pool margin and of the turf of vegetation round it so as to leave old tussocks of vegetation lying in the midst of the mud surface of the pools. These disintegrate gradually, and often the last sign of them is a slightly raised tussock of *Eriophorum*.

The area indicated by Figs. 20 and 21 together is considered to represent a wide transition region from the more centrally placed *Sphagnetum* to the more marginally placed *rand* where pools are abundant.

(iv) *Pools "partly filled with Sphagnum"*

The title stands for those pools which show a definite marginal colonization by *Sphagnum*; it would include, for instance, pools with a 5–10 cm. wide belt of *S. cuspidatum*, or one with a wide belt of *S. pulchrum* or *papillosum*, leaving only a small bare area in the centre. Pools of this type are rarely linked and are deeper and much softer than those already described. When bare mud is exposed, as the result of fine weather conditions, it is soft and brown in colour, in contrast to the firm black surface seen in the more marginal pool types. The region of abundance of this type of pool, as shown in Fig. 22, lies internally to the zones so far described, but does not extend across the geometrical centre of the bog surface.

(v) *Less than 15% of the area covered by pools more than 30 cm. across*

The region shown in Fig. 23 is roughly complementary to that shown in Fig. 22, and is clearly made up of two components, one central, the other marginal. The central area corresponds to the region where nearly all the pools that are present are filled with *Sphagnum*. It is taken as defining the limits of the *Scirpetum* and *Molinietum* together. The marginal zone represents the lower *rand* vegetation where pools are entirely absent.

(vi) *Living Sphagnum abundant in the surface cover*

Fig. 24 is mainly concerned with the peat building *Sphagna*, *S. papillosum* and *S. pulchrum*, since *S. cuspidatum* and *S. tenellum* were not considered in making the percentage estimation. It includes the lesser quantities of *S. rubellum*, *S. plumulosum* and *S. medium* which may go to make up the general *Sphagnum* carpet.

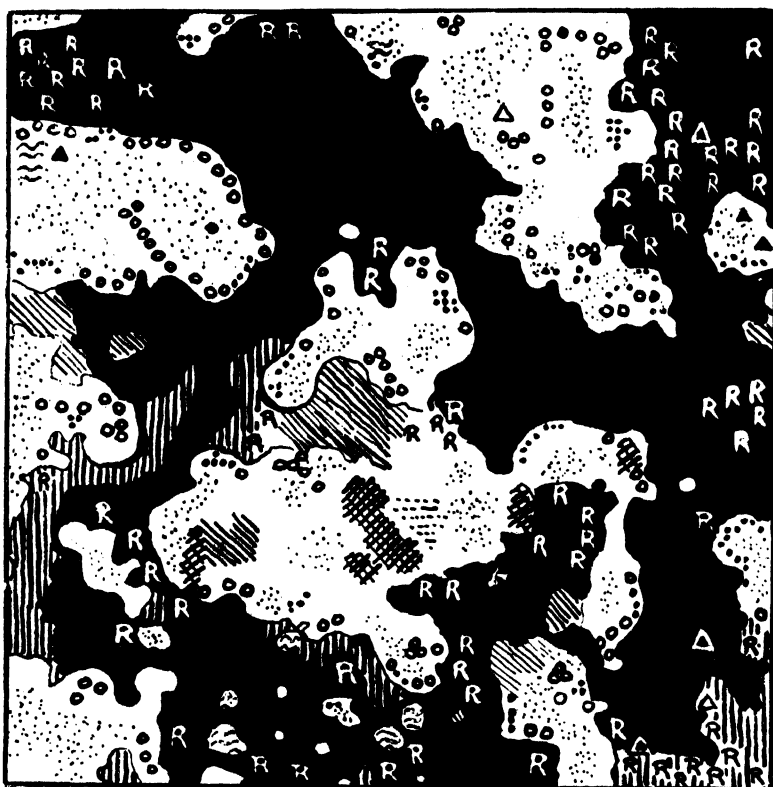


FIG. 30. 5 m. quadrat in the upper rand, where pools show much bare mud and are usually linked. (Quadrat 9, position, K 0.)

While there seem to be two distinct regions with maximum abundance, i.e. values above 15%, the inclusion of values from 10 to 15% suggests that the *Sphagnum*-rich region genuinely encircles the central region of the bog.

Moreover this encircling zone coincides, within the limit of error, with the zone given by Fig. 22, where *Sphagnum* is actively colonizing pools, and the two characters considered together are taken to be the criterion of the Sphagnetum community. Some such criterion is essential in order to arrive at the distribution map given in Fig. 4, for the Sphagnetum merges into the neighbouring associations so gradually that it is impossible to locate the transition when walking over the bog surface itself.

(vii) *Sphagnum pulchrum*

This species is confined to the Regeneration Complex, the most strongly characterized expression of the Sphagnetum. It was estimated on a frequency scale of 0–3, the value 1 indicating very rare occurrence, as for instance, one patch of the species in any particular length of transect. Fig. 25 shows the fairly well defined limits of its distribution.

(viii) *Softness*

If an observer on treading in a pool sank rapidly above the ankles or further, the pool fell under the definition of “soft”. In any section of a transect a note was made as to whether the majority of the pools were soft (s.) or the majority firm (f.); where the numbers were about equal, “f. to s.” was recorded. Regions recorded as “s.” are shown black in Fig. 26, those as “f. to s.” are stippled. Here again there is a clearly limited distribution illustrating the much softer nature of the pools and general ground-surface in the Regeneration Complex. The limits of the latter community may be defined by the combined data of Figs. 25 and 26.

(ix) *Molinia*

Fig. 27 is perhaps one of the most interesting of the series, showing as it does the dual nature of the distribution of *Molinia* on the bog. The species was estimated on a frequency scale of 0–5, as a component of the general surface cover, but was disregarded when it only occurred as a constituent of the “island” flora. The central region of abundance delimits the Molinietum; the marginal area of distribution covers the rand as a whole, and that part of it where *Molinia* attains dominance represents the lower rand vegetation.

It is noteworthy that although the few species associated with *Molinia* in the lower rand—*Potentilla erecta* for instance—are found again in the central Molinietum, the two communities are quite distinct in character, as one might expect, considering the difference in their positions in relation to the bog as a whole. The difference lies partly in the softer nature of the ground in the central Molinietum and partly in the abundance of *Betula* and of species such as *Empetrum nigrum*, and various *Bryophyta* which are lacking from the rand association.

(x) *Cladonia*

The irregularity exhibited by Fig. 28 in the distribution of maximum abundance of *Cladonia* is due again to personal error but is not sufficient to obscure the main conclusion that *Cladonia* flourishes especially round the bog margin and at the northern end described as the Callunetum. The latter is one of the worst defined communities, partly because it is really only an extreme variant of the rand vegetation, partly because it is disturbed and

irregular and lacking in well defined floral characteristics, and partly because it lies on the limit of the region investigated by quantitative methods. For the sake of definition it may be distinguished as that part of the rand in which *Cladonia sylvatica* forms 15% or more of the surface cover. The extent of the rand itself is defined by the presence of *Molinia* and of drainage channels.

VII. WATER-LEVELS AND THE DISTRIBUTION OF PLANT COMMUNITIES

It is a very natural supposition that the water-level relationships should play a large part in determining the distribution of different types of mire vegetation, and indeed the distinctive zonation of the rand in a raised bog is obviously so controlled. In order, therefore, to gather preliminary data on this important issue, in the 1937 excursion an extensive series of water-level pits was made. At each of thirty-five sites two separate pits were dug; average soil-level along their sides was estimated and marked by reference stakes driven laterally into the walls. Over a period of several days the water-level in relation to average soil-level was recorded in each of these pits. The thirty-five pits were distributed at intervals of 100 m. along two offset lines *G* and *K*, which cross the long axis of the bog, and along a line parallel to the base line and 400 m. west of it, i.e. more or less down the long axis of the bog. The positions are shown in Fig. 31, and the communities in which the different sites lie can be seen from Fig. 4.

In Fig. 32 are given the results for the four days 5–9 July. Two readings are given for each site for each day and a smoothed curve connects all the readings for each day. The readings show simply the distance of the water-level below mean soil-level in the pits. Above each set of curves has been shown the approximate range of the vegetation types traversed. Consideration will show a marked correlation between the vegetation type and position of the water-table.

Along offset *K* it is evident that the water-table lies lowest under the rand and is nearest the surface in the Sphagnetum. The centre of the bog (along this line) is occupied by Scirpetum and Molinietum which are drier than the Sphagnetum. Although the curves along offset *G* differ in shape from those along *K* they show a similar relationship to the vegetation. The rand at either end is well-drained but here, at the eastern end, there is a strongly marked fluctuation probably related to the marginal drainage system. The whole of the line from 200 to 800 m. shows high water-levels: most of this wet region is well-developed Regeneration Complex, but between 200 and 400 m. is an area transitional between Sphagnetum and Scirpetum.

The line down the long axis of the bog begins from the extremely gentle rand-slope where the bog meets the hillside on its north-east face: it is not surprising that the water-level is high here. At the same time the highest maintained levels lie between *C* and *H* through strongly developed Regenera-

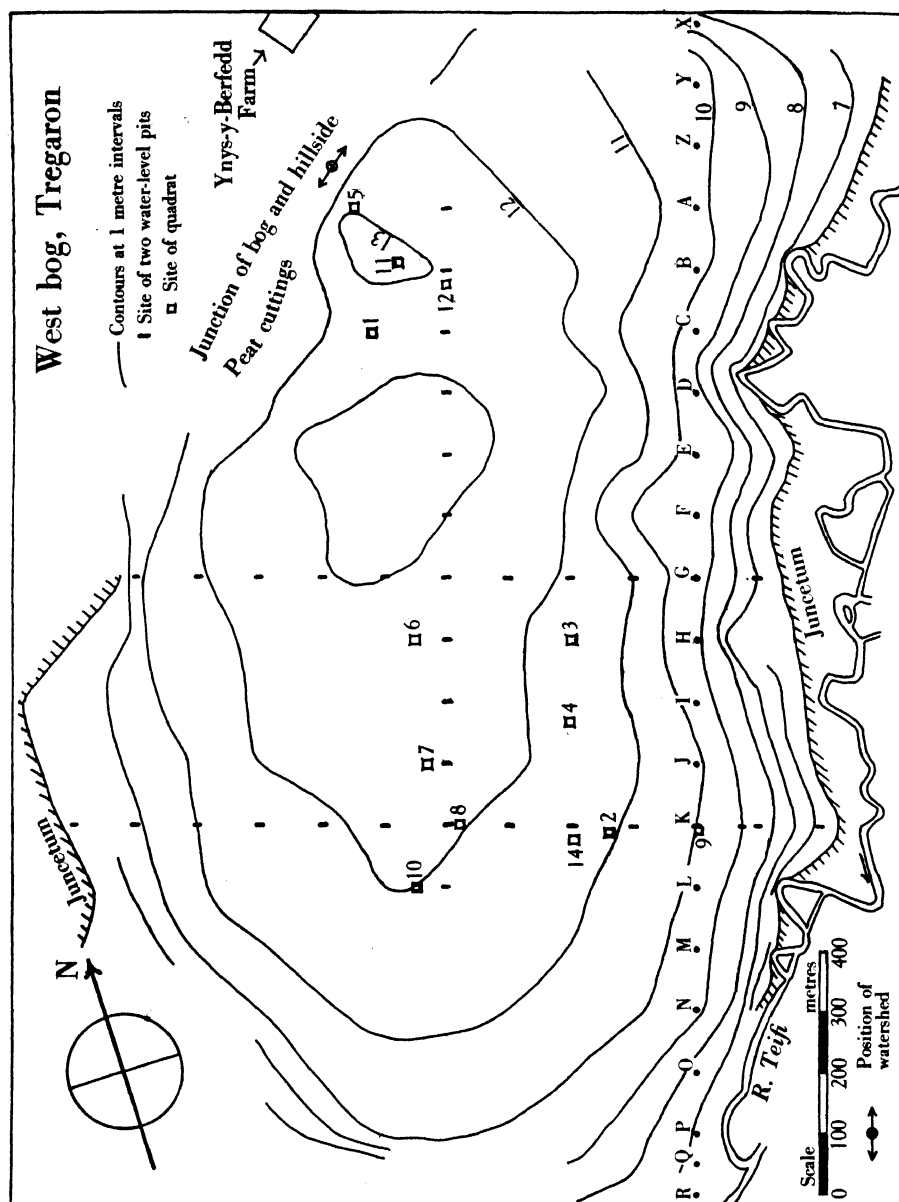


FIG. 31. Contour map of the bog, giving positions of water level pits and quadrats.

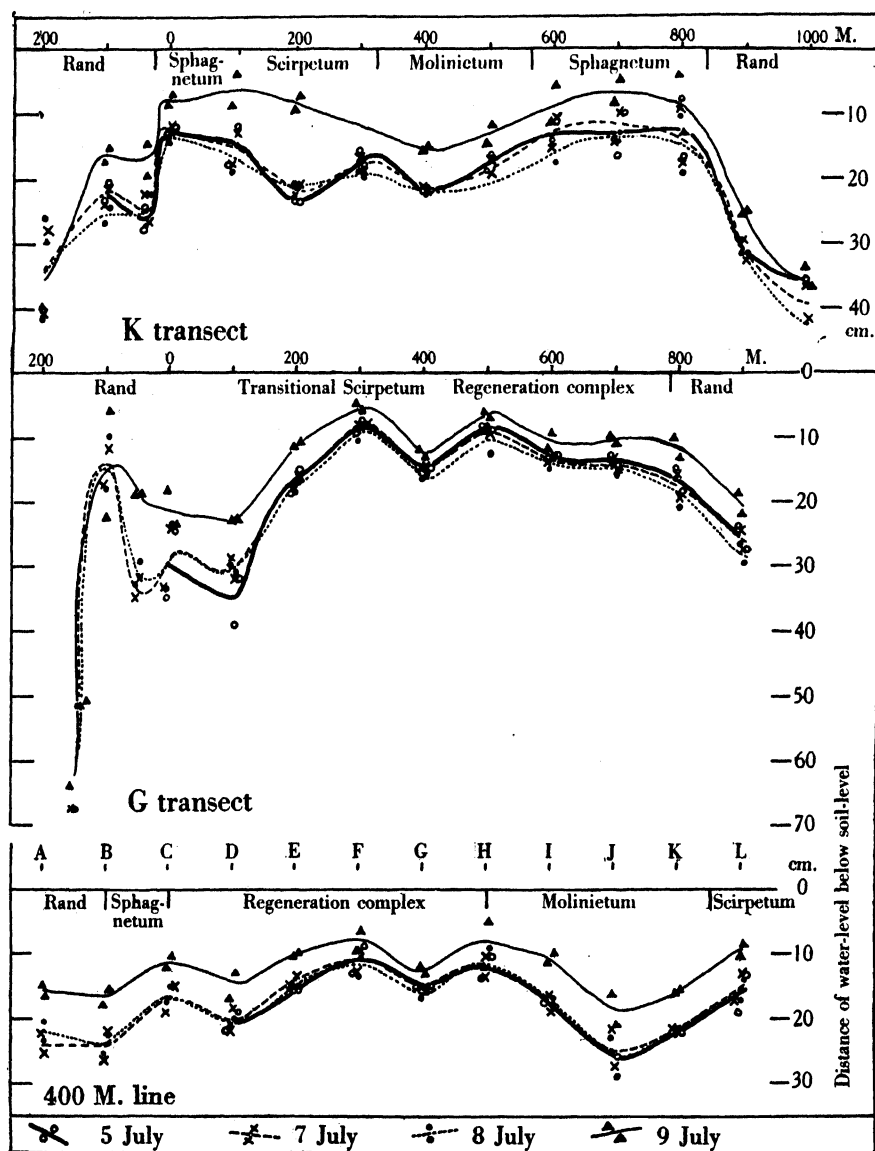


FIG. 32. Diagram showing water-level relationships of the bog in July 1937. In each figure is shown the distance of water-level below soil-level at the water-level pits distributed in pairs over the bog surface.

tion Complex. It is very striking that between *H* and *L*, where there is Molinietum, the water-levels are much lower.

It should be noted that these levels were taken after a rather long rainless period and that they represent the bog in a dry state, although the readings for 9 July represent the effect of a day's heavy rain. Much as we should like to know the behaviour of the water-table in more prolonged drought, and at other and wetter times of year, the data are nevertheless sufficient to suggest a broad relationship with the plant communities. At dry times the wettest communities are the Regeneration Complex and the very similar Sphagnetum; the Scirpetum is rather drier and the Molinietum markedly so; the rand is naturally the driest. This, of course, accords with the disposition of zones from top to bottom of the rand itself, from a Sphagnetum, through Scirpetum to Molinietum, in a sequence of increasing dryness.

It is at once evident from Fig. 4 that the Regeneration Complex lies close to the north-western margin of the bog, and it seems very likely that it owes this position to the increased wetness caused by the gentle transition to the steep hill side and consequent feeble development of a rand and its marginal drainage systems. A further feature of the greatest theoretical interest is the disposition of Sphagnetum in a wide band round the bog within the rand, and surrounding a centre of Scirpetum and Molinietum, both communities markedly drier than the Sphagnetum. One feels at once that no explanation of the present disposition of communities on the bog surface can afford to neglect this feature of the bog hydrography.

Our own explanation is admittedly hypothetical, but can, we think, be supported by much indirect evidence. It is based on a frank recognition that raised bogs are long-lived structures capable not only of growing in favourable climatic conditions, but of persisting through considerable periods unfavourable to them. It has indeed long been known that in their strata they reflect former conditions of growth and arrest: Granlund has established synchronous "recurrence surfaces" very widely in the bogs of south-east Sweden, and it has been actually shown in the Tregaron bog itself that a "retardation layer" forms a very conspicuous band of humified peat in the otherwise very fresh and undecomposed upper *Sphagnum* peat (Godwin & Mitchell, 1938). That this layer was a climatic effect is made more probable by the fact that it occurs in *all three* of the separate raised bogs in the Teifi valley at Tregaron, and there can be little doubt that it represents a phase of arrested bog development. The degree of humification of the peat is so great, unfortunately, that its analysis gives no clear index to the communities which formed it, but they clearly cannot have been Sphagneta, and were probably drier communities produced by drying of the bog surface in a less wet climatic period, or possibly in a more continental one.

From our recognition of this fact it follows that bogs are not all necessarily growing now, nor need their communities be entirely explicable in

terms of present conditions. During a sufficiently wet period we can suppose that a raised bog develops its maximum convexity. The crown of the bog even in summer is not dried out, and the whole centre of the bog is covered with the Regeneration Complex, like most of the great "red bogs" of the central Irish plain at the present day. Only the marginal portions are so steep that the surface streams cut channels into them, drain them and cause them to bear drier communities such as *Scirpeta*, *Calluneta* and *Molinieta*¹. The disposition of surface and water-level is that shown in Fig. 33a. During an ensuing dry period it is not really known what happens to the bog, but it loses water by transpiration and evaporation faster than it receives it (at least for part of the year). This must cause a general lowering of the water-

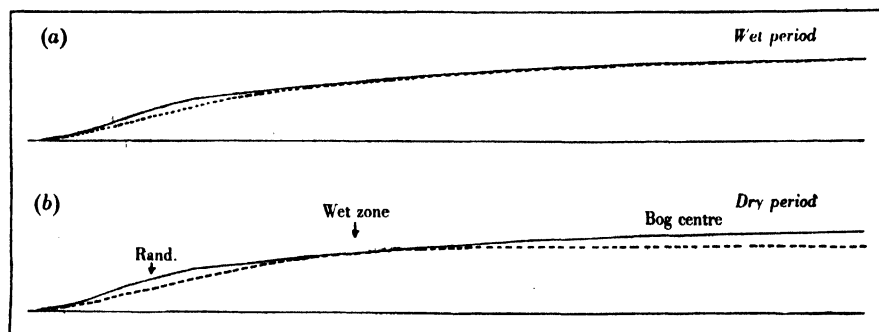


FIG. 33. Hypothetical behaviour of the water-table in a raised bog in wet and in dry climatic periods. The actual surface profile is that of the western bog along transect 9.

table which will naturally soonest affect the highest central portions of the bog surface. The lower marginal parts remain wet as before, supplied by the main reservoir of the higher parts of the bog, for though flatter than before the water surface in the bog is still convex. That a flow does take place from the centre outwards is shown by the maintenance of springs at the foot of the rand. The rand drainage channels mostly carry water shed directly from the bog surface and flowing superficially. In a dry period then the surface and water-levels are those shown in Fig. 33b. This provides a dry centre to the bog and a wetter periphery. The apparent anomaly of a *drier* zone, the rand, still lower on the margin, is due to the local steepness and erosion of streams, which provide a cover of a few feet of especially well-drained peat above the sloping margin of the water-table.

From this explanation of the disposition of the bog communities it follows that we must regard the West Bog at Tregaron as at present suffering, or very recently having suffered, a period of climatic dryness. A very interesting chain of evidence lends support to such a view. Since we always had in mind the

¹ It is possible that the bog margins also develop their greatest steepness during wet climatic periods and that in succeeding dry periods they become dried out and eroded.

likelihood that the bog history would be recorded in its stratigraphy, we attempted on many occasions to discover the nature of the peat immediately below the *Scirpetum* or *Molinietum*. To our surprise the sections always showed a sharp discontinuity: a very short depth below the surface was almost pure *Sphagnum* peat in a moderately fresh condition. This invariably turned out to be *S. imbricatum* peat, a fact of special significance since despite prolonged search, no single plant of this species was ever found on the living bog surface. This fact alone argues some sharp discontinuity between present conditions and former history of the bog. Moreover, this discontinuity extends

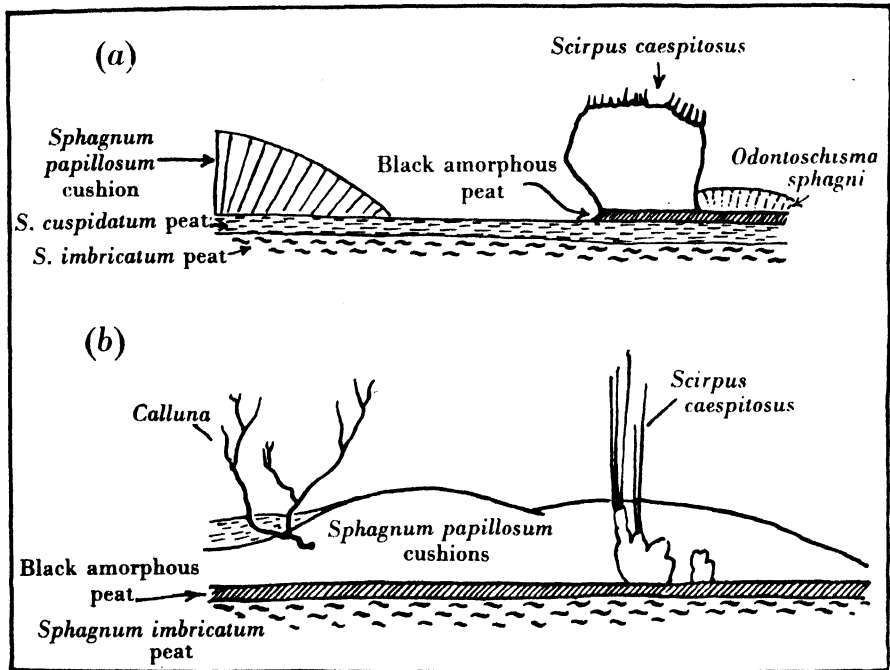


Fig. 34. Diagrams of soil profiles showing transition from underlying *Sphagnum imbricatum* peat to the most recent peat immediately below the existing vegetation.

to those parts of the bog which are now wet. Fig. 34 shows the result of careful excavation in the Regeneration Complex: here also *S. imbricatum* peat immediately underlies the present hummocks and pools, sometimes separated therefrom by a layer of black amorphous peat with abundant thick stems of *Calluna*. It is quite clear that the vegetation structure is being re-established over an old drier surface, and probably represents some degree of renewed bog-growth after a phase of retardation or standstill which is still expressed by the drier communities of the bog centre. The bog has in fact just formed, and perhaps still is forming, a retardation layer like that present lower down in the young *Sphagnum* peat of all three Tregaron bogs. It should be noted

that this older retardation layer disappeared diffusely at the margins of the south-eastern bog, in just the way which would seem likely if dryness most affects the bog centre.

The most obvious criticism which can be made against an interpretation in terms of climatic change is that similar effects may have been caused by artificial drainage induced by peat-cutting or by burning. Against this it may be said that *marginal* drainage, such as would follow from peat-cuttings, is not likely to cause a dry centre and a wet periphery. Moreover, the whole of the eastern margin of the bog shows an undisturbed rand, but shows the phenomena of dryness equally on the eastern as on the western bog surface. Finally, and perhaps most strikingly, it must be pointed out that this recent disappearance of *Sphagnum imbricatum* from raised bogs is by no means limited to this bog. The upper *Sphagnum* peat of most English raised bogs recently investigated is overwhelmingly made of *S. imbricatum*. We have found this in all three bogs at Tregaron, in the raised bogs of the Somerset levels, Fenn's Moss, Shropshire, Borth Bog, Cardiganshire, and Dr Blackburn informs us that it is true also for other bogs in the north of England. Nevertheless living *S. imbricatum* is either very rare or quite absent where a living *Sphagnum* cover still exists. Furthermore, an exactly parallel situation exists in the raised bogs of Holland, and has already been commented upon (Florschütz, 1932).

S. imbricatum is a markedly oceanic species and only a climatic shift towards dryness or increased continentality seems suitable to explain its widespread and simultaneous disappearance. It seems highly likely that the drying of the bog surfaces which we suppose to have set in was also responsible for the virtual disappearance of the water-loving *Scheuchzeria palustris* which was abundant in the earlier sub-Atlantic Danish peats.

It is, of course, well known that other authors, on other grounds, have suggested that a recent return to drier conditions has followed the extreme wetness of the sub-Atlantic (e.g. Szafer, from beech distribution, 1935).

The utilization of *Sphagnum imbricatum* prompts a mention of two other species which also have an interesting relation to the bog surface. The first is *S. medium*, another markedly oceanic species which is only locally abundant in this bog, although very widespread on many Irish raised bogs. It is here limited as an active tussock-former to certain parts of the Regeneration Complex. The other species is the shrub *Myrica gale*, which is entirely absent from Tregaron bog although exceedingly abundant in the raised bog at Borth, not far to the north.

It is interesting, in the light of our present interpretation of recent bog history, to recall the comments made in describing the Regeneration Complex (p. 327) to the effect that stages of pool invasion were very frequent and degenerate tussocks very infrequent. This departure from expectation is not remarkable if the Regeneration Complex is only just re-establishing itself over an older drier surface. We feel that possibly similar anomalies not only in

Tregaron, but in other West European bogs, could be resolved by recognizing the importance of recent climatic fluctuation.

VIII. SUMMARY

This paper deals with the ecology of a raised bog (raised moss or "Hochmoor") developed in the valley of the river Teifi, just north of the village of Tregaron, Cardiganshire.

A contour map was made of the bog, which was thus shown to be domed, but to pass very gradually into hillside on its north-western side. Near this junction was a definite lagg.

The vegetation of the bog is described under the headings, Lagg, River-terrace, Rand, Sphagnetum and Regeneration Complex, Scirpetum, Molinietum, and Callunetum. It was shown that the structure of the Regeneration Complex corresponds substantially with that already described by Osvald for other raised bogs both in Sweden and elsewhere.

The large size of the bog made special survey methods essential, and these were based on a grid of one hundred metre squares spread over most of the bog. Quantitative eye estimations of suitable indices to the surface ecology were collected by parallel transects across the bog, and these permitted the construction of index maps bringing out certain striking features of vegetational distribution.

Initial measurements of the water-level were made at thirty-five sites on the bog surface and showed the Regeneration Complex and Sphagnetum to occupy wetter areas than the Scirpetum and Molinietum which grow in the centre of the bog. In order to explain the presence of these drier communities in this position, a hypothesis is put forward that the bog is suffering, or has recently suffered, a period of climatic dryness or continentality in which the bog-centre has dried out. Support in favour of this hypothesis is the discontinuity of the surface vegetation from the peat just below it, which is composed very largely of *Sphagnum imbricatum*, a species now quite absent from the living cover of the bog.

REFERENCES

- Florschütz, F. *et al.* "Resultate von Untersuchungen an einigen Niederländischen Mooren." *Rec. Trav. bot. néerland.* **29**, 1932.
- Godwin, H. & Mitchell, G. F. "Stratigraphy and development of two raised bogs near Tregaron, Cardiganshire." *New Phytol.* **37**, 425, 1938.
- Osvald, H. *Myrar och Myrödling*. Stockholm, 1937.
- Szafer, Wl. "The significance of isopollen lines for the investigation of the geographical distribution of trees in the post-Glacial Period." *Bull. int. Acad. Cracovie*, B, 1935.

APPENDIX. ANNOTATED LIST OF THE BRYOPHYTA ON
TREGARON WEST BOG

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THE Bryophyta of the bog are numerous and interesting, not only because several of them are dominants of certain facies of the bog vegetation, but because the bog offers a great variety of habitats of small area, which may be occupied by the less conspicuous Bryophyta that are associated with the major communities. One may divide the Bryophyta into two groups on this ecological basis:

Group (a). Those which, owing to size, vigour or habit, take a place in the community which is equivalent to that of the majority of the phanerogams, and compete with these.

Group (b). The smaller bryophytes which live in habitats provided by the phanerogams and the bryophytes of group (a). Their environment is controlled to a great extent by the larger plants and in their distribution they are closely connected with them. The smaller habitats may be classified roughly as follows:

- (1) Amongst *Sphagnum pulchrum*.
- (2) Amongst *S. papillosum*.
- (3) Amongst *S. plumulosum*.
- (4) Amongst *S. cuspidatum*.
- (5) In narrow gaps between tussocks.
- (6) On vertical sides of tussocks.
- (7) On sloping sides of tussocks.
- (8) On crowns of *Scirpus* tussocks.
- (9) On crowns of tussocks with *Calluna*.

This division is not altogether satisfactory; for example, *Sphagnum cuspidatum* offers a very different habitat according to whether it is in a deep growth in a pool which remains wet till late on in the season, or whether it is in a thin layer on a rapidly drying pool. Tussock sides offer rather different habitats according as the tussocks are close together or isolated. Some of the above names are self-explanatory.

Straight sides of tussocks are found where the tussocks have sharp vertical edges of bare peat, as though eroded. Such tussocks may be on the edges of true pools, or they may be close together, leaving small wet hollows up to say 15 cm. across between them. These are the *narrow gaps between tussocks*. Sometimes there are gently sloping bare peaty sides to a tussock. These are *sloping sides*.

Crowns of tussocks with Calluna. *Calluna* bushes are usually growing on an irregular peaty mound—often much eroded. There is often some *Scirpus*, etc., also present but typically sparse and weak. Habitats 6, 7 and 9 are all essentially bare peat habitats. Habitat 5 is in some ways a semi-aquatic habitat, while in the others the substrate is essentially formed by the living plants.

The *Molinia* communities of the rand are exceedingly poor in Bryophytes: little is found here except *Calypogeia trichomanis* and perhaps a few fragments of *Dicranum scoparium*. It is noteworthy also that patches of *Rhacomitrium*, *Hypnum schreberi* and *Hylocomium splendens* are completely free from any admixture of other species, in strong contrast with the tussocks of *Sphagna* and *Leucobryum*, in which small Hepatics abound. This list of Bryophyta is as far as possible complete for the raised bog proper; a number of common species from the lagg and the peat cuttings have been omitted, though some of the more interesting species from the latter are included. No ecological notes are given for the species belonging to group (a) above, since these are included in the descriptions of the major plant communities which they characterize. Exceptions to this have been made in the case of species of group (a) which under some circumstances behave as though they belonged to group (b).

SPHAGNA

S. fimbriatum. Very rare on the bog, and practically confined to *Molinia* islands. A few stems were found in one locality only outside an island.

S. rubellum.

S. plumulosum.

S. squarrosum. Very rare in the bush-grown part of the lagg on the north-west margin of the bog. Gathered by D. H. Valentine.

S. amblyphyllum. Bright green forms are very abundant in the lagg. They vary much in robustness, and the stem leaves vary in obtuseness, some approaching *S. recurvum*. A pinkish brown form is found on the raised bog and is confined to "islands". It has been recorded from lines *D*, 400, *I*, c. 600, and *R*, 25–55.

S. pulchrum.

S. tenellum.

S. cuspidatum.

S. inundatum. Rare in the southern part of the bog, and confined to occasional small, steep-sided deep pools. It is common throughout the northern part of the bog, in steep-sided deep pools and in winding channels.

S. papillosum.

S. medium.

It is worth noting that submerged forms of *S. tenellum*, *S. plumulosum* and *S. papillosum* were gathered growing with tall *S. cuspidatum* and *S. inundatum* in a deep ditch in the north-west part of the bog.

HEPATICAE

Aneura sinuata. Apparently widespread, but in very minute amounts only. Usually on bare peat in the tops of tussocks with *Calluna*; more rarely amongst mosses such as *Sphagnum papillosum*.

Gymnocolea inflata. Seen mainly in the southern part of the bog, where it is not uncommon, especially in the *Scirpetum*, in which it frequently covers the floors of narrow gaps and small wet hollows between *Scirpus* tussocks. It is also to be found on sloping margins of pools.

Lophozia ventricosa. Rare and usually in small amounts; probably however widespread. On old tussocks of *Scirpus*, *Calluna* or *Molinia*; was seen covering a decaying tussock of the latter.

Lophozia incisa. Probably widespread but rare and in very small bits. Usually on wet bare peat of eroding *Calluna* tussocks, etc., more rarely amongst *Sphagna*.

Leptoscyphus anomalus. Common over the whole bog. Scattered stems creep over the surface of the drier *Sphagnum* cushions (*S. papillosum*, *S. plumulosum*, *S. rubellum*), or over bare peat surfaces of eroding areas, etc. Common on the tops of tussocks with *Calluna*, and also on vertical edges of tussocks.

Cephalozia bicuspidata. Frequent, and in considerable variety of habitat, but usually not in large quantity. Frequent in *Sphagnum cuspidatum* and *S. plumulosum*; has been recorded from *S. pulchrum*. Often on the edges of small pools, and on the moist lower slopes of sloping or straight tussock sides.

Cephalozia connivens. Rare and in very small amounts. In *Sphagnum plumulosum*, or on moist bare peat. Seen on level surfaces of bare peat in the old cuttings in the north bog.

Cephalozia fluitans. Common amongst *Sphagna*. Most commonly amongst *S. pulchrum* or in pools amongst *S. cuspidatum*, and in these it was only found where the pools were still wet in July. It is much rarer in *S. papillosum*, and is perhaps mainly found in this habitat in the wetter western part of the bog.

Cephalozia species. No fertile material was found; species therefore uncertain. Not uncommon in minute amounts amongst *Sphagna* and *Leucobryum*.

Odontoschisma sphagni. Very abundant over most of the bog. Creeping in isolated stems over the drier tops of cushions of *Sphagnum papillosum*, *S. rubellum*, *S. medium*, *S. plumulosum*, *Leucobryum*, etc., or when luxuriant forming loose mats over these; stems creeping over bare eroding peat of tussock sides, etc.; abundant in the tops of tussocks with *Scirpus* or *Calluna*. Often forming loose cushions in narrow gaps and irregular hollows between tussocks.

Odontoschisma denudatum. Confined to the northern part of the bog where it is rather rare but widespread, on hard bare peat of denuding *Calluna* tussocks.

Calypogeia trichomanis. Rather rare. In tussock tops with *Scirpus* or *Calluna*; on old *Molinia* tussocks.

Calypogeia fissa. Rather rare; habitat as last, and also in scattered stems amongst *Sphagnum plumulosum*, *S. pulchrum* and *Leucobryum*.

Lepidozia setacea. Very abundant. In very slender stems interwoven amongst *Sphagna* (especially *S. papillosum* and *S. plumulosum*) and *Leucobryum*; in great abundance in the tops of tussocks with *Scirpus* and *Calluna*, and on vertical sides.

Diplophyllum albicans. Very abundant. In the tops of tussocks with *Calluna* and *Scirpus*; in *Eriophorum* tussocks; narrow gaps between tussocks; more rarely amongst *Sphagna*.

MUSCI

Polytrichum strictum.

Polytrichum commune. Confined to "islands".

Campylopus flexuosus. Rare, especially on old *Molinia* tussocks. Also on tops and sloping edges of *Scirpus* tussocks.

Leucobryum glaucum.

Dicranum scoparium.

Racomitrium lanuginosum.

Aulacomnium palustre.

Webera nutans. Rather rare and in small quantity; on decaying or eroding tussocks.

Mnium cinclidioides. Locally very abundant amongst *Juncus acutiflorus* in ditches in the old peat cuttings.

Hypnum cupressiforme var. *ericetorum*.

Hypnum cordifolium. Locally abundant in ditches on old peat cuttings.

Hypnum schreberi.

Hylocomium splendens.

The nomenclature used for mosses is that of H. H. Dixon (*The Students' Handbook of British Mosses*, 3rd. Edn., 1924), and for hepatics that of MacVicar (*The Students' Handbook of British Hepatics*, 2nd. Edn., 1926).

SOME MARINE ALGAL COMMUNITIES OF GREAT CUMBRAE

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(With two Figures in the Text)

INTRODUCTION

A SURVEY of the algal vegetation of a portion of the coast of the island of Great Cumbrae, Firth of Clyde, was carried out during the period March 1935 to March 1937, for comparison with the vegetation of Castletown Bay, Isle of Man, where a survey had already been made (Gibb, 1938). A study of the chief algal communities has been undertaken particularly in regard to their vertical and horizontal distribution and their seasonal changes.

The portion of shore selected for detailed examination is situated at the north end of the island (Fig. 1). It extends from a point north-east of Wine Bay to a short distance south-west of Eerie Port (Fig. 2), i.e. a strip of coast-line over $\frac{1}{2}$ mile long. The shore, whilst chiefly rocky, includes several large sandy and pebble-strewn areas. The maximum width is about 300 ft., where the slope is fairly gentle, the steepest parts occurring on either side of Wine Bay and Eerie Port. Levels were obtained throughout the area by observation of the sea-level simultaneously on a tide gauge at Keppel Pier and at certain positions in the survey area itself.

PHYSICAL CONDITIONS

The island of Great Cumbrae occupies a sheltered position in the Firth of Clyde. The influence of wind, however, on a partly enclosed sea area such as this is considerable, as it produces irregularities in the tidal range by acceleration or retardation of the tidal flow. Such irregularities have an effect on the vertical distribution of the algal vegetation. The survey area is exposed chiefly to west, north-west and north winds. Since the prevailing wind on the west coast of Scotland is south-west, the area, as a whole, is not frequently exposed to heavy seas. Winds from other directions have only a small effect because of the shelter afforded by surrounding land. This feature and the fairly gentle slope tend to reduce the splash zone above high-water mark.

Sea-temperature records at Keppel Pier show that a mean maximum temperature of 13.6° C. occurs in August and a mean minimum of 6.6° C. in February. The mean temperature of the air at Rothesay (M.O. 407, 1936) is

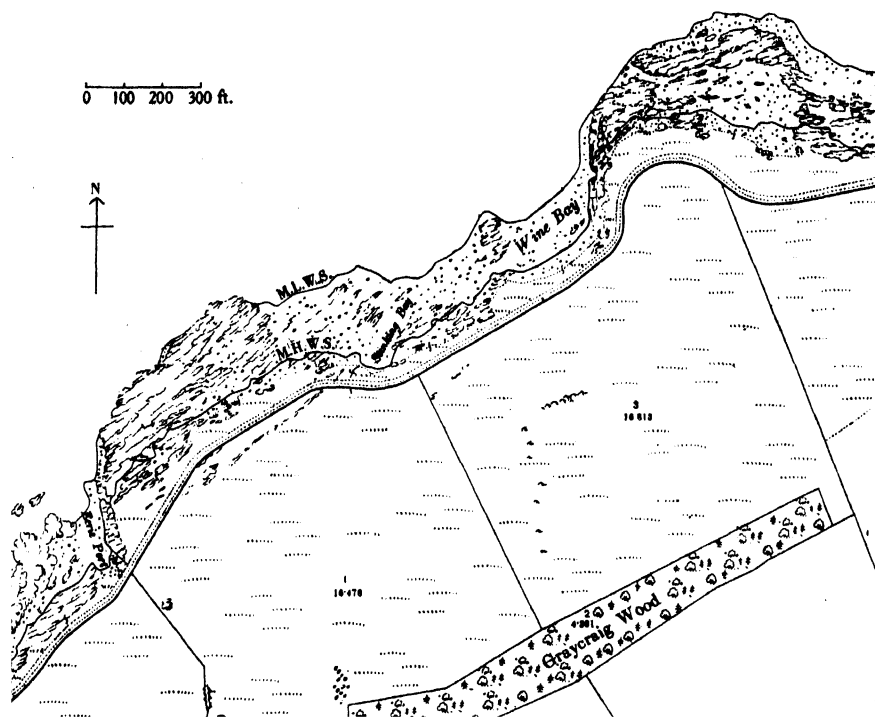
A map of the Clyde region in Scotland. The map shows the following features:

- Islands:** Kintyre, Arran, Bute, and Gt. Cumbrae.
- Rivers:** Loch Fyne, R. Clyde, and the Firth of Clyde.
- Towns and Locations:** Bute, Rothersey, Knock Hill Station, Gt. Cumbrae, and Keppel.
- Other Labels:** Kintyre, Arran, Firth of Clyde, Ayrshire, Channel, and a scale of miles (0 to 6).
- Orientation:** A north arrow is located in the bottom left corner.

The water of the Firth of Clyde has a high salinity. According to Mill (1892) the average percentage of pure sea water ($s=35\text{ ‰}$) at Knock Hill, the nearest station to the north of Great Cumbrae, is 94.3% throughout the whole depth and 90.5% in the surface layer. At several points of the survey area there are small streams, the largest of which lies near the eastern boundary of

the area. Definite changes in the vegetation occur in the vicinity of these streams.

The tidal range at ordinary spring tides is 10 ft. High water occurs almost simultaneously throughout the Firth of Clyde, and the tidal streams are mostly moderate in speed (*West Coast of Scotland Pilot*, 1934). The tidal stream which



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Fig. 2. Map of survey area at north Cumbrae.

passes eastward of the Cumbrae islands has a maximum rate of 2 knots at spring tides, whilst the greatest rate of the stream on the westward side is $1\frac{1}{2}$ knots. These streams unite northward of the Cumbrae islands and run at a greatest rate of 1 knot towards the lochs higher up the firth. The time of high water at full and change of the moon is 11 hr. 50 min., thus low water of spring tides occurs about 6 o'clock morning and evening.

The levels throughout this paper are given in feet above (+) or below (–) mean sea-level, the tidal levels for Cumbrae being as follows:

Mean high-water springs (M.H.W.S.)	+ 5 ft.
Mean high-water neaps (M.H.W.N.)	+ 3 ft.
Mean sea-level (M.S.L.)	0 ft.
Mean low-water neaps (M.L.W.N.)	– 3 ft.
Mean low-water springs (M.L.W.S.)	– 5 ft.

A comparison of the areas surveyed on Cumbræ and at Castletown Bay in the Isle of Man shows that in general the littoral zone is much narrower in the former area. This difference is chiefly due to the considerably smaller tidal range in the Firth of Clyde which is 10 ft. (3 m.) at ordinary spring tides as compared with 18 ft. (5.5 m.) at Castletown Bay. Exposure to wind and wave action is much greater at Castletown Bay, but differences in sea and air temperatures between the two places are so small as to be negligible. There is a considerable difference in the amount of sunshine, however, Rothesay having an average of 1274 hr. per annum as compared with 1574 hr. at Douglas, Isle of Man (M.O. 408, 1936).

THE ALGAL COMMUNITIES

The chief communities of the area are the following:

I. *Communities of rocky shores.*

- A. *Enteromorpha intestinalis* community.
- B. *Porphyra-Urospora-Ulothrix* community.
- C. *Pelvetia-Fucus spiralis* community.
- D. *Ascophyllum* community.
- E. *Laurencia* community.
- F. *Fucus vesiculosus* community.
- G. *Gigartina-Cladophora* community.
- H. *Enteromorpha Linza* community.
- J. *Fucus serratus* community.
- K. *Laminaria* community.
- L. Pool vegetation.

II. *Communities of sand, mud and pebbles.*

- M. *Pelvetia canaliculata* var. *coralloides* community.
- N. *Chaetomorpha-Vaucheria* community.
- O. *Rhodochoorton* community.
- P. Sand-pool vegetation.
- Q. *Laminaria saccharina* community.

I. *Communities of rocky shores*

A. *Enteromorpha intestinalis* community.

A dense pure growth of *Enteromorpha intestinalis* is found above high-water mark of spring tides in many parts of the area. It occurs chiefly in small patches on parts of the rock surface which are kept moist by land drainage, but it is also abundant near the edge of brackish pools. The community persists at all seasons of the year but is most conspicuous in early summer. By the end of the summer much of the *Enteromorpha* has disappeared owing to drought.

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This community was recorded also for Castletown Bay, where it grows extensively on a substratum of stones and pebbles in the vicinity of a small fresh-water stream.

B. *Porphyra-Urospora-Ulothrix community.*

This community is found on smooth rock surfaces near high-water mark of spring tides. Its distribution is irregular and it is best developed on the fairly steep parts of the shore west of Eerie Port and between Stinking Bay and Eerie Port. The community is seasonal, appearing in winter and spring, the maximum crop occurring in March. The most abundant species are *Porphyra umbilicalis* var. *linearis*, *Urospora isogona* and *Ulothrix flacca*, but they vary in relative abundance in different parts of the area. Additional species which are generally present are *Bangia fusco-purpurea*, *Enteromorpha intestinalis*, *Oscillatoria* sp., *Prasiola stipitata* and *Ulothrix implexa*.

This community is not so well developed on the sheltered shore of Cumbrae as on the exposed rocky shore at Castletown Bay where it covers large areas of the sloping ledges between high-water mark of neap and spring tides. Moreover, a distinct zonation of the species occurs at Castletown Bay, but this is absent in the Cumbrae community.

C. *Pelvetia-Fucus spiralis community.*

This is one of the most extensive communities in the area. It occupies a zone between +2.6 and +5 ft. on all the rocky parts of the shore, and at some places where the *Ascophyllum* zone is small it extends even lower. *Fucus spiralis* is the dominant species throughout the greater part of the community, the *Pelvetia* being dominant only in a narrow zone at the upper limit. The undergrowth is rather sparse except in the lower part of the community and includes the following species:

<i>Catenella repens</i> (whole year)	<i>Gigartina stellata</i> (whole year)
<i>Chaetomorpha linum</i> (whole year)	<i>Leathesia difformis</i> (summer)
<i>Cladophora flexuosa</i> (spring and summer)	<i>Monostroma Grevillei</i> (spring)
<i>C. rupestris</i> (whole year)	<i>Ralfsia verrucosa</i> (whole year)
<i>Enteromorpha compressa</i> (whole year)	<i>Rivularia atra</i> (whole year)

The community is much better developed here than at Castletown Bay, where it is present only in the more sheltered parts of the area and occupies a smaller vertical zone.

D. *Ascophyllum community.*

Ascophyllum nodosum grows abundantly on the gently sloping parts of the area but is practically absent from the steepest parts immediately east of both Wine Bay and Eerie Port. The zone dominated by this alga extends at some points from -2.2 to +2 ft., although the species is usually most abundant in the upper part of the zone; at lower levels the plants are often sparse and are mixed with *Fucus serratus* and *F. vesiculosus*. *Polysiphonia fastigiata* occurs frequently on *Ascophyllum*, especially on plants in the lower part of the zone. The characteristic undergrowth which accompanies *Ascophyllum* consists largely

of *Cladophora rupestris*. The full list of species is given in Table I which shows also their seasonal occurrence.

Table I. *Species forming the undergrowth of the Ascophyllum community*

Species	Sp.	S.	A.	W.
<i>Ceramium rubrum</i> Ag.	o.	o.	o.	o.
<i>Chaetomorpha linum</i> Kütz.	o.	o.	o.	o.
<i>Chondrus crispus</i> Stackh.	o.	o.	o.	o.
<i>Cladophora albida</i> Kütz.	—	o.	—	—
<i>C. flexuosa</i> Harv.	f.	f.	—	o.
<i>C. rupestris</i> Kütz.	a.	a.	a.	a.
<i>Cladostephus spongiosus</i> Ag.	o.	o.	o.	o.
<i>Cruoria pellita</i> Lyngb.	o.	o.	o.	o.
<i>Gelidium corneum</i> Lamour.	o.	o.	o.	o.
<i>G. crinale</i> J. Ag. var. <i>genuinum</i> Hauck	o.	o.	o.	o.
<i>Gigartina stellata</i> Batt.	f.	f.	f.	f.
<i>Isthmoplea sphaerophora</i> Kjellm.	f.	—	—	—
<i>Laurencia pinnatifida</i> Lamour.	o.	o.	o.	o.
<i>Leathesia difformis</i> Aresch.	—	f.	—	—
<i>Lithothamnion Lenormandi</i> Fosl. var. <i>squamulosa</i> Fosl.	f.	f.	f.	f.
<i>Monostroma Grevillei</i> Wittr.	f.	—	—	—
<i>Ulva lactuca</i> L. var. <i>latissima</i> DC.	o.	—	—	o.

d. = dominant, cd. = co-dominant, a. = abundant, f. = frequent. o. = occasional, l. = locally, Sp. = Spring, S. = Summer, A. = Autumn, W. = Winter.

This community is not so well represented on Cumbrae as on the sheltered northern part of the Castletown Bay survey area, where a considerable degree of shelter and a very gently sloping shore apparently favour its development.

E. *Laurencia community*.

This distinctive community occurs only in small patches on sloping rock at a few places between the levels +0.2 and +2.4 ft. It is composed entirely of small algae which form a short dense growth completely covering the rock surface. *Laurencia pinnatifida* is dominant but *Cladophora rupestris* occurs abundantly. The community undergoes considerable seasonal change owing to influxes of short-lived species which occur chiefly as epiphytes on the more permanent vegetation. The species which form the community, together with their frequency and seasonal occurrence, are given in Table II.

Table II. *Species forming the Laurencia community*

Species	Sp.	S.	A.	W.
<i>Callithamnion Hookeri</i> Ag.	—	—	o.	—
<i>Ceramium acanthonotum</i> Carm.	o.	o.	—	—
<i>C. rubrum</i> Ag.	f.	f.	f.	f.
<i>C. strictum</i> Harv.	—	f.	f.	—
<i>Chaetomorpha linum</i> Kütz.	o.	o.	o.	o.
<i>Chondrus crispus</i> Stackh.	o.	o.	o.	o.
<i>Cladophora albida</i> Kütz.	—	f.	—	—
<i>C. flexuosa</i> Harv.	f.	o.	—	—
<i>C. lanosa</i> Kütz.	a.	a.	a.	a.
<i>Corallina officinalis</i> L.	f.	f.	f.	f.
<i>Gigartina stellata</i> Batt.	o.	o.	o.	o.
<i>Isthmoplea sphaerophora</i> Kjellm.	f.	—	—	—
<i>Laurencia pinnatifida</i> Lamour.	d.	d.	d.	d.
<i>Leathesia difformis</i> Aresch.	o.	a.	o.	—
<i>Lithothamnion Lenormandi</i> Fosl. var. <i>squamulosa</i> Fosl.	f.	f.	f.	f.
<i>Monostroma Grevillei</i> Wittr.	f.	—	—	—
<i>Porphyra leucosticta</i> Thur.	f.	—	—	—
<i>Rivularia atra</i> Roth.	o.	o.	o.	o.

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This community closely resembles the *Laurencia-Lomentaria* community at Castletown Bay where, however, it is much more extensive and includes abundant *Lomentaria articulata*.

F. *Fucus vesiculosus* community.

A few small areas situated between Stinking Bay and Eerie Port and lying between the levels -1.4 and $+0.9$ ft. are dominated by *Fucus vesiculosus*. The plants grow on barnacle-covered rock and are unaccompanied by other species. A little epiphytic *Elachistea fucicola* is often present on the *Fucus*.

At Castletown Bay the community is much better developed, occurring below the *Ascophyllum* zone on the exposed part of the ledges, and above it on the sheltered part of the area.

G. *Gigartina-Cladophora* community.

This is one of the most characteristic communities on the steeper parts of the shores ranging from -3.2 to $+1$ ft. On the more gentle slopes it is largely replaced by the *Fucus serratus* and *Ascophyllum* communities, but even in these it persists to some extent as undergrowth. The co-dominant species, *Gigartina stellata* and *Cladophora rupestris*, are very conspicuous, *Gigartina* chiefly in the lower and *Cladophora* in the upper part of the zone. It was found, however, that the relative abundance of the two species depended largely on exposure and slope. *Gigartina* flourishes on the steepest and most exposed slopes where there is much splash while *Cladophora* predominates on the more gently sloping parts of the rock. During spring and summer *Ceramium acanthonotum* is abundant. Table III gives the frequency and seasonal distribution of the species comprising the community, and it will be seen that the majority belong to the Rhodophyceae.

Table III. *Species forming the Gigartina-Cladophora community*

Species	Sp.	S.	A.	W.
Callithamnion Hookeri Ag.	f.	f.	f.	f.
Ceramium acanthonotum Carm.	a.	a.	o.	f.
C. flabelligerum J. Ag.	—	o.	—	o.
C. rubrum Ag.	f.	f.	f.	f.
Chaetomorpha linum Kütz.	f.	—	o.	—
Cladophora rupestris Kütz.	cd.	cd.	cd.	cd.
Delesseria alata Lamour.	—	—	—	o.
D. ruscifolia Lamour.	o.	—	—	—
Gigartina stellata Batt.	cd.	cd.	cd.	cd.
Lithothamnion Lenormandi Fosl. var. squamulosa Fosl.	f.	f.	f.	f.
Lomentaria articulata Lyngb.	o.	o.	o.	o.
Monostroma Grevillei Wittr.	f.	—	—	—
Phycodrys rubens Batt.	o.	—	—	—
Plumaria elegans Schm.	f.	f.	f.	f.
Polysiphonia Brodiaei Grev. var. typica Holm. & Batt.	—	—	f.	—
P. nigrescens Grev.	f.	f.	f.	f.
P. urceolata Grev.	o.	—	o.	—
Porphyra leucosticta Thur.	—	o.	—	—
Pylaiella littoralis Kjellm.	f.	—	—	—
Trailliella intricata Batt.	f.	f.	o.	o.

This community is not represented at Castletown Bay, but similar communities dominated by *Gigartina* have been described for other coasts. According to Cotton (1912) and Rees (1935) *Gigartina* communities occur frequently in west and south-west Ireland. Börgesen (1905) records a *Gigartina* "association" as one of the commonest communities on the coasts of the Faeröes, and Jónsson (1912) states that it is widely distributed in Iceland. Its occurrence also in west Norway has been mentioned by Kylin (1910) and others.

H. *Enteromorpha Linza* community.

During spring and summer several small local developments of this community occur at the level of low-water neaps. Their appearance is usually connected with the presence of some sand on the rock surface, and the community constantly undergoes change in composition owing to most of the species being short-lived spring and summer annuals. In spring there is no single dominant, although a few species occur in considerable quantity, e.g. *Cladophora arcta*, *Monostroma Grevillei* and *Polysiphonia urceolata*. Throughout the summer *Enteromorpha Linza* is dominant and *Cladophora albida* abundant. The list of species is given in Table IV.

Table IV. *Species forming the Enteromorpha Linza community*

Species	Spring	Summer
<i>Ceramium strictum</i> Harv.	—	o.
<i>Chordaria flagelliformis</i> Ag.	—	f.
<i>Cladophora albida</i> Kütz.	—	a.
<i>C. arcta</i> Kütz.	a.	f.
<i>C. rupestris</i> Kütz.	f.	f.
<i>Dumontia incrassata</i> Lamour.	o.	f.
<i>Enteromorpha compressa</i> Grev.	o.	—
<i>E. Linza</i> J. Ag. var. <i>lanceolata</i> Kütz.	f.	d.
<i>Eudesme virescens</i> (Carm.) J. Ag.	—	o.
<i>Gigartina stellata</i> Batt.	o.	o.
<i>Isthmoplea sphaerophora</i> Kjellm.	o.	o.
<i>Leathesia difformis</i> Aresch.	—	o.
<i>Monostroma Grevillei</i> Wittr.	a.	—
<i>Phyllitis fascia</i> Kütz. var. <i>genuina</i> Batt.	f.	—
<i>Polysiphonia nigrescens</i> Grev.	o.	o.
<i>P. urceolata</i> Grev. var. <i>typica</i> J. Ag.	a.	f.
<i>Porphyra leucosticta</i> Thur.	f.	f.
<i>Punctaria plantaginea</i> Grev.	—	f.
<i>P. tenuissima</i> Grev.	—	f.
<i>Pylaiella littoralis</i> Kjellm.	f.	f.
<i>Scytosiphon lomentarius</i> J. Ag.	f.	f.
<i>Ulva lactuca</i> L. var. <i>latissima</i> DC.	o.	o.

This community is similar to the *Enteromorpha-Cladophora-Chordaria* community found on the ledges at Castletown Bay. Both communities are associated with sand-covered rock near low-water mark of neap tides and many of the species are common to both. The Castletown Bay community, however, is the more extensive and includes a larger number of species.

J. *Fucus serratus* community.

Fucus serratus occurs throughout the area with the exception of the very steepest slopes. It is not an abundant species except on the gently sloping

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regions east of Wine Bay and west of Stinking Bay where it occurs between the levels -4.8 and -2.2 ft. On steeper slopes it does not range higher than -3 ft.

The species is usually accompanied by some *Ascophyllum*, a little *Fucus vesiculosus* and a remarkably constant and characteristic subvegetation composed of the following:

Callithamnion Hookeri	f.	Cruoria pellita.	f.
Ceramium rubrum	f.	Delesseria alata	f.
Chondrus crispus	f.	Dumontia incrassata	o.
Cladophora albida	o.	Gigartina stellata	a.
C. rupestris	a.	Lithothamnion Lenormandi var. squamulosa	a.
Cladostephus spongiosus	f.	L. polymorphum	o.

Several species occur as epiphytes on *Fucus serratus*, e.g. *Ceramium rubrum*, *Ectocarpus tomentosus*, *Elachistea fucicola*, *Enteromorpha compressa*, *Porphyra leucosticta* and *Sphacelaria cirrhosa* var. *fusca*.

Fucus serratus appears to flourish best on a very gently sloping rocky shore where there is a moderate amount of shelter.

K. *Laminaria community.*

This community extends from -4 ft. downwards into the sublittoral region and is present throughout the survey area except where the substratum is sandy; there it gives place to the *Laminaria saccharina* community. *L. digitata* is the dominant species but below low-water springs it is mixed with some *L. Cloustoni*. The latter is irregular in its distribution and the plants are poorly developed. The undergrowth throughout the community includes a large number of species, mostly Rhodophyceae. The following occur:

Ceramium rubrum	f.	Lomentaria clavelliosa	f.
Chondrus crispus	f.	Mesogloia vermiculata	o.
Cladophora lanosa	o.	Odonthalia dentata	o.
C. rupestris	f.	Phycodrys rubens	f.
Cruoria pellita	f.	Phyllophora membranifolia	f.
Cystoclonium purpureum	f.	Plumaria elegans	o.
Delesseria alata	f.	Polysiphonia elongata	o.
D. ruscifolia	f.	P. urceolata var. typica	f.
D. sanguinea	o.	Porphyra leucosticta	f.
Dilsea edulis	f.	Rhodochorton Rothii	o.
Gigartina stellata	a.	Rhodophyllis bifida	o.
Lithothamnion Lenormandi var. squamulosa	f.	Rhodymenia palmata	f.
L. polymorphum	a.	Ulva lactuca var. latissima	f.
Lomentaria articulata	o.		

Certain characteristic epiphytes occur on the *Laminariae*. Those found on *L. digitata* are *Ceramium rubrum*, *Ectocarpus fasciculatus*, *Enteromorpha compressa*, *Polysiphonia urceolata*, *Porphyra leucosticta*, *Rhodymenia palmata* var. *marginifera* and *Ulva lactuca* var. *latissima*. The epiphytes on *Laminaria Cloustoni* differ somewhat from those on *L. digitata* and are as follows: *Cladophora rupestris*, *Delesseria alata*, *Dermatolithon macrocarpum* var. *Laminarii*, *Ectocarpus fasciculatus*, *Polysiphonia urceolata*, *Ptilota plumosa* and *Rhodymenia palmata* var. *marginifera*. At Castletown Bay the epiphytes on

the stipes of *Laminaria Cloustoni* showed a definite zonation but this was not apparent on the poorly developed Cumbrae plants, although they are practically identical in both localities.

The *Laminaria* community at Cumbrae is dominated by *L. digitata* throughout, thus differing from the community at Castletown Bay where two zones are distinguishable, the lower dominated by *L. Cloustoni* while *L. digitata* is confined to an upper zone.

L. Pool vegetation.

Numerous pools occur throughout the survey area and belong to two distinct types, namely, "coralline" pools, containing much *Corallina* and *Lithothamnion*, and sand-pools. The "coralline" type is least frequent in the area and occurs chiefly on the steeper parts of the shore. Below the level of low-water mark of neap tides (— 3 ft.) all the pools are of the sand-pool variety. A description of the sand-pool flora is given later (pp. 376–80), as it belongs to the second group of communities.

The "coralline" pools are mostly rather shallow and contain numerous species many of which are annual and short-lived. Table V shows the species which occur in the pools at different levels and seasons of the year. Species of *Lithothamnion*, in most cases, cover much of the rock surface in these pools, while certain characteristic perennial species, e.g. *Corallina officinalis*, *Chondrus crispus* and *Cladophora rupestris*, are constantly present in the pools at all levels. In the case of certain of the pool species, e.g. *Dumontia incrassata* and *Scytosiphon lomentarius*, there is a definite migration of successive generations up and down the shore. The direction of these migrations at different seasons can be seen from Table V.

At Castletown Bay rock pools are far more numerous than at Cumbrae and are chiefly of the "coralline" type. The flora of the pools is much alike in both places, however, although *Corallina* is more abundant at Castletown.

II. Communities of sand, mud and pebbles

M. *Pelvetia canaliculata* var. *coralloides* community.

This is a salt-marsh community which occurs just above h.w.s.t. level in many parts of the survey area, chiefly where the slope is gentle. It occupies the seaward muddy margins of the grassy banks and is quite extensive at a few points covering areas about 12 ft. (4 m.) in width where the slope is very gentle. The dominant species is *Pelvetia canaliculata* var. *coralloides*, a limnicolous variety of *Pelvetia* first recorded by Baker (1912) for the sheltered salt marshes at Blakeney Point, Norfolk. The plants, about 1 cm. long, are crowded together, forming a dense mossy turf. The substratum consists of thick sandy mud in which the plants are partly embedded. Numerous plants of *Statice maritima* and *Salicornia europaea* grow amongst the *Pelvetia*. Several other

Table V. *Vegetation of "coralline" rock pools*

Species	Season	Level		
		+5 to +3 ft.	+3 to 0 ft.	0 to -3 ft.
<i>Callithamnion Hookeri</i> Ag.	Sp.	—	o.	f.
	S.	—	—	f.
	A.	—	o.	f.
	W.	—	o.	f.
<i>Ceramium rubrum</i> Ag.	Whole year	—	f.	f.
<i>C. strictum</i> Harv.	Sp.	—	o.	—
	S.	—	o.	f.
	A.	—	—	—
	W.	—	—	—
<i>Chaetomorpha tortuosa</i> Kütz.	Sp.	—	f.	o.
	S.	—	f.	o.
	A.	—	o.	o.
	W.	—	o.	—
<i>Chondrus crispus</i> Stackh.	Whole year	o.	o.	o.
<i>Cladophora albida</i> Kütz.	Sp.	—	—	—
	S.	—	f.	f.
	A.	—	—	—
	W.	—	—	—
<i>C. arcta</i> Kütz.	Sp.	—	—	o.
	S.	—	—	o.
	A.	—	—	—
	W.	—	—	—
<i>C. rupestris</i> Kütz.	Whole year	f.	a.	f.
<i>C. sericea</i> Kütz.	Sp.	a.	f.	—
	S.	a.	f.	—
	A.	—	—	—
	W.	—	—	—
<i>Corallina officinalis</i> L.	Whole year	o.	a.	f.
<i>Cruoria pellita</i> Lyngb.	Whole year	—	f.	f.
<i>Cystoclonium purpureum</i> Batt.	Sp.	—	o.	f.
	S.	—	—	a.
	A.	—	—	o.
	W.	—	o.	o.
<i>Delesseria alata</i> Lamour.	Whole year	—	—	o.
<i>Dictyota dichotoma</i> Lamour.	Whole year	—	a.	f.
<i>Dilsea edulis</i> Stackh.	Whole year	—	—	o.
<i>Dumontia incrassata</i> Lamour.	Sp.	f.	f.	o.
	S.	—	f.	f.
	A.	—	—	—
	W.	o.	o.	—
<i>Enteromorpha Linza</i> J. Ag. var. <i>lanceolata</i> (Kütz.)	Sp.	—	—	f.
	S.	—	—	f.
	A.	—	—	—
	W.	—	—	—
<i>Eudesme virescens</i> (Carm.) J. Ag.	Sp.	—	—	o.
	S.	—	o.	f.
	A.	—	—	—
	W.	—	—	—
<i>Fucus serratus</i> L.	Whole year	—	o.	f.
<i>Gigartina stellata</i> Batt.	Whole year	—	f.	f.
<i>Halidrys siliquosa</i> Lyngb.	Whole year	—	l.a.	o.
<i>Laminaria digitata</i> Lamour. var. <i>typica</i> Fosl.	Whole year	—	o.	f.
<i>Laurencia hybrida</i> Lenor.	Sp.	—	f.	o.
	S.	—	o.	—
	A.	—	o.	—
	W.	—	—	o.
<i>Leathesia difformis</i> Aresch.	Sp.	—	o.	o.
	S.	—	f.	f.
	A.	—	o.	—
	W.	—	—	—
<i>Lithophyllum incrustans</i> Fosl.	Whole year	—	f.	o.
<i>Lithothamnion Lenormandi</i> Fosl.	Whole year	o.	f.	f.

Table V (cont.)

Species	Season	Level		
		+ 5 to + 3 ft.	+ 3 to 0 ft.	0 to - 3 ft.
Lithothamnion polymorphum Aresch.	Whole year	—	—	f.
Lomentaria articulata Lyngb.	Whole year	—	—	o.
Monostroma Grevillei Wittr.	Sp.	a.	f.	f.
	S.	—	—	—
	A.	—	—	—
	W.	—	—	—
M. latissimum Wittr.	Sp.	—	—	f.
	S.	—	—	—
	A.	—	—	—
	W.	—	—	—
Nitophyllum ramosum Batt.	Whole year	—	—	o.
Phycodrys rubens Batt.	Whole year	—	—	o.
Phyllitis fascia Kütz. var. genuina Batt.	Sp.	—	—	f.
	S.	—	—	—
	A.	—	—	—
	W.	—	—	—
Plumaria elegans Schm.	Whole year	—	—	f.
Polysiphonia elongata Grev.	Sp.	—	o.	f.
	S.	—	—	o.
	A.	—	o.	o.
	W.	—	—	o.
P. nigrescens Grev.	Sp.	o.	f.	a.
	S.	—	f.	a.
	A.	—	f.	a.
	W.	—	f.	f.
P. urceolata Grev. var. typica J. Ag.	Sp.	—	—	f.
	S.	—	—	f.
	A.	—	—	—
	W.	—	—	o.
Porphyra leucosticta Thur.	Sp.	—	o.	f.
	S.	—	o.	o.
	A.	—	—	—
	W.	—	—	—
Pterosiphonia parasitica Schm.	Whole year	—	—	o.
Rhomomela subfusca Ag.	Sp.	—	f.	f.
	S.	—	—	a.
	A.	—	—	f.
	W.	—	o.	a.
Scytosiphon lomentarius J. Ag.	Sp.	f.	o.	f.
	S.	o.	o.	f.
	A.	a.	f.	—
	W.	a.	o.	—
Sphacelaria cirrhosa Ag. var. fusca Holm. & Batt.	Whole year	—	o.	o.
S. cirrhosa Ag. var. pennata Hauck	Whole year	o.	o.	o.
Trailiella intricata Batt.	Sp.	—	—	o.
	S.	—	—	f.
	A.	—	—	o.
	W.	—	—	o.
Ulva lactuca L. var. latissima DC.	Whole year	—	—	o.

species of algae also occur, e.g. much *Enteromorpha Ralfsii*, *Rhizoclonium riparium* and *Rivularia nitida* as well as some *Achinetospora pusilla* var. *crinita*, *Percursaria percursa* and *Vaucheria* sp. These algae apparently colonize the bare muddy portions first before *Pelvetia* has become established.

Vegetation of this nature does not occur at Castletown Bay. Cotton (1912) appears to have been the first to describe a community of its kind, namely, the "*Fucus vesiculosus* var. *muscoides* association", of western Ireland. Later,

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Baker & Bohling (1915) described this type of vegetation for Norfolk and Rees (1935) for south-west Ireland.

N. *Chaetomorpha-Vaucheria* community.

On the gently sloping portion of shore at the extreme north-east part of the survey area, between +3 and +5 ft., much of the rock surface lies beneath a thick layer of fine sand. The bare rocky parts are occupied by the *Pelvetia-Fucus spiralis* community already described, while a *Chaetomorpha-Vaucheria* community develops on the sandy portions. The dominant species are *Chaetomorpha linum* and *Vaucheria Thuretii*, much of the former being present throughout the year while the latter is most abundant in summer. Other species included in this community are:

Cladophora sericea (Sp.)
Dumontia incrassata (Sp.)
Enteromorpha intestinalis (whole year)
Monostroma Grevillei (W. and Sp.)

Phyllitis fascia var. *genuina* (W. and Sp.)
Rhizoclonium implexum (S.)
R. Kochianum (S.)
Scytosiphon lomentarius (whole year)

Several of the species of the community, e.g. *Chaetomorpha linum*, *Cladophora sericea*, *Rhizoclonium implexum*, *R. Kochianum* and *Vaucheria Thuretii*, are unattached to any solid substratum, being more or less immersed in the sand. The remaining species are attached to small pebbles.

No similar community was found at Castletown Bay, but the "*Vaucheria Thuretii* association" described by Cotton (1912) for western Ireland has much in common with this Cumbrae community.

O. *Rhodochorton* community.

Several small areas dominated by *Rhodochorton Rothii* occur between the levels -1.5 and +0.9 ft. on flat or gently sloping rock beside sandy parts of the shore. The *Rhodochorton*, which is attached to the rock either in the form of small tufts or as a dense mossy covering, retains quantities of sand. *Pringsheimia scutata* is a common epiphyte on *Rhodochorton* at all seasons. Species of *Cladophora* grow abundantly in this community, e.g. *C. rupestris* at all seasons, *C. arcta* in spring and *C. flexuosa* in summer. Much seasonal change is apparent in the community, the details of which are given in Table VI.

The *Laurencia-Cladophora-Rhodochorton* community at Castletown Bay has several features in common with this community. It occurs on a similar substratum of sand-covered rock and includes many of the same species.

P. *Sand-pool* vegetation.

Sand-pools are very common in the survey area at all levels of the shore; below low-water mark of neap tides every pool contains much sand. The vegetation of these pools often appears to be unattached, but this is not actually the case since the plants are usually anchored to rock below the sand or to pebbles. The sand-pool flora differs markedly from that of the "coralline" pools already described. About half of the species found in the sand-pools do

Table VI. *Species forming the Rhodochorton community*

Species	Sp.	S.	A.	W.
<i>Ceramium acanthonotum</i> Carm.	—	f.	—	—
<i>Chaetomorpha linum</i> Kütz.	o.	o.	o.	o.
<i>Cladophora arcta</i> Kütz.	a.	o.	—	—
<i>C. flexuosa</i> Harv.	f.	a.	—	f.
<i>C. rupestris</i> Kütz.	a.	a.	a.	a.
<i>Cladostephus spongiosus</i> Ag.	f.	f.	f.	f.
<i>Enteromorpha compressa</i> Grev.	f.	o.	o.	o.
<i>E. clathrata</i> J. Ag. var. <i>genuina</i> Batt.	f.	—	—	—
<i>Gelidium crinale</i> J. Ag. var. <i>genuinum</i> Hauck	o.	o.	o.	o.
<i>Gigartina stellata</i> Batt.	o.	o.	o.	o.
<i>Isthmoplea sphaerophora</i> Kjellm.	f.	—	—	—
<i>Laurencia pinnatifida</i> Lamour.	o.	o.	o.	o.
<i>Leathesia difformis</i> Aresch.	—	f.	—	—
<i>Monostroma Grevillei</i> Wittr.	f.	—	—	—
<i>Porphyra leucosticta</i> Thur.	f.	f.	—	—
<i>Pringsheimia scutata</i> Rke.	f.	f.	f.	f.
<i>Pylaiella littoralis</i> Kjellm.	f.	f.	—	o.
<i>Rhizoclonium Kochianum</i> Kütz.	o.	o.	o.	o.
<i>Rhodochorton Rothii</i> Näg.	d.	d.	d.	d.
<i>Sphacelaria cirrhosa</i> Ag. var. <i>fusca</i> Holm. & Batt.	f.	f.	f.	f.
<i>Ulva lactuca</i> L. var. <i>latissima</i> DC.	o.	—	o.	o.

not occur in the "coralline" pools, and seasonal change is very apparent in the former owing to many species being short-lived. At certain seasons the flora of some pools comprises only a very few species while at other times the same pools have a rich and varied vegetation. Table VII shows the vertical distribution and seasonal occurrence of the sand-pool species.

Table VII. *Vegetation of sand-pools*

Species	Season	Level			
		+ 5 to + 3 ft.	+ 3 to 0 ft.	0 to - 3 ft.	- 3 to - 5 ft.
<i>Ahnfeldtia plicata</i> Fries.	Whole year	—	o.	o.	f.
<i>Asperococcus fistulosus</i> Hook.	Sp.	—	o.	—	—
	S.	—	a.	f.	f.
	A.	—	o	—	—
	W.	—	—	—	—
	Sp.	f.	f.	—	—
<i>Chaetomorpha aerea</i> Kütz.	S.	f.	—	—	—
	A.	f.	f.	—	—
	W.	a.	f.	o.	—
	Whole year	—	o.	o.	f.
	Sp.	—	—	—	—
<i>Chondrus crispus</i> Stackh.	S.	—	—	—	f.
<i>Chorda filum</i> Stackh.	A.	—	—	—	—
	W.	—	—	—	—
	Sp.	—	—	—	o.
	S.	—	o.	o.	f.
	A.	—	o.	o.	a.
<i>Chordaria flagelliformis</i> Ag.	W.	—	—	—	—
	Sp.	—	—	—	—
	S.	—	o.	o.	—
	A.	—	o.	o.	—
	W.	—	—	—	—
<i>Cladophora albida</i> Kütz.	Sp.	—	—	—	—
	S.	—	f.	f.	—
	A.	—	—	—	—
	W.	—	—	—	—
	Sp.	—	—	—	o.
<i>C. lanosa</i> Kütz.	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—
	Whole year	o.	a.	f.	f.

Table VII (cont.)

Species	Season	Level			
		+5 to +3 ft.	+3 to 0 ft.	0 to -3 ft.	-3 to -5 ft.
<i>C. sericea</i> Kütz.	Sp.	a.	f.	o.	—
	S.	f.	f.	o.	—
	A.	—	—	—	—
	W.	—	—	—	—
<i>Corallina officinalis</i> L.	Whole year	—	o.	o.	o.
<i>Cruoria pellita</i> Lyngb.	Whole year	—	o.	o.	f.
<i>Cystoclonium purpureum</i> Batt.	Sp.	—	—	—	f.
	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Delesseria hypoglossum</i> Lamour.	Sp.	—	—	—	f.
	S.	—	—	—	—
	A.	—	—	—	—
	W.	—	—	—	—
<i>D. sanguinea</i> Lamour.	Sp.	—	—	—	f.
	S.	—	—	—	—
	A.	—	—	—	—
	W.	—	—	—	—
<i>Dictyosiphon foeniculaceus</i> Grev.	Sp.	—	—	o.	—
	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Dumontia incrassata</i> Lamour.	Sp.	—	f.	f.	o.
	S.	—	o.	f.	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Ectocarpus confervoides</i> Le Jol.	Sp.	—	—	—	—
	S.	—	f.	—	—
	A.	—	o.	—	—
	W.	—	—	—	—
<i>Enteromorpha intestinalis</i> Link.	Whole year	a.	—	—	—
<i>E. Linza</i> J. Ag. var. <i>lanceolata</i> (Kütz.)	Sp.	—	—	f.	—
	S.	—	—	f.	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Eudesme virescens</i> (Carm.) J. Ag.	Sp.	—	—	—	—
	S.	—	o.	o.	o.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Fucus serratus</i> L.	Whole year	—	f.	f.	f.
<i>Furcellaria fastigiata</i> Lamour.	Whole year	—	—	—	f.
<i>Gigartina stellata</i> Batt.	Whole year	—	o.	f.	f.
<i>Gracilaria confervoides</i> Le Jol.	Sp.	—	—	—	—
	S.	—	—	—	o.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Halidrys siliquosa</i> Lyngb.	Whole year	—	—	—	f.
<i>Laminaria digitata</i> Lamour. var. <i>typica</i> Fosl.	Whole year	—	—	—	f.
	Whole year	—	—	—	f.
<i>L. saccharina</i> Lamour.	Whole year	—	—	—	f.
<i>Leathesia difformis</i> Aresch.	Sp.	—	f.	—	—
	S.	—	a.	f.	f.
	A.	—	o.	o.	—
	W.	—	—	—	—
<i>Litosiphon filiformis</i> Batt.	Sp.	—	—	—	—
	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>L. pusillus</i> Harv.	Sp.	—	—	—	—
	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—

Table VII (*contd.*)

Species	Season	Level				
		+ 5 to	+ 3 ft.	+ 3 to 0 ft.	0 to - 3 ft.	- 3 to - 5 ft.
<i>Lomentaria clavellosa</i> Gail.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	—
	A.	—	—	—	—	o.
	W.	—	—	—	—	f.
<i>Mesogloia vermiculata</i> Le Jol.	Sp.	—	—	—	—	—
	S.	—	—	—	o.	f.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Monostroma Grevillei</i> Wittr.	Sp.	—	—	f.	o.	o.
	S.	—	—	—	—	o.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Myriotrichia clavaeformis</i> Harv.	Sp.	—	—	—	—	—
	S.	—	—	f.	—	—
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>M. filiformis</i> Harv.	Sp.	—	—	—	—	—
	S.	—	—	f.	—	—
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Nitophyllum punctatum</i> Grev.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	—
	A.	—	—	—	—	o.
	W.	—	—	—	—	f.
<i>N. ramosum</i> Batt.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	o.
	A.	—	—	—	—	o.
	W.	—	—	—	—	—
<i>Phycodrys rubens</i> Batt.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	o.
	A.	—	—	—	—	o.
	W.	—	—	—	—	f.
<i>Phyllitis fascia</i> Kütz. var. <i>genuina</i> Batt.	Sp.	—	—	f.	f.	—
	S.	—	—	—	—	—
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Phyllophora membranifolia</i> J. Ag.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	o.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Polyides rotundus</i> Grev.	Whole year	—	—	—	—	f.
<i>Polysiphonia elongata</i> Grev.	Sp.	—	—	—	—	f.
	S.	—	—	—	—	f.
	A.	—	—	—	—	o.
	W.	—	—	—	—	o.
<i>P. nigrescens</i> Grev.	Whole year	—	—	o.	o.	f.
<i>Porphyra leucosticta</i> Thur.	Sp.	—	—	f.	—	—
	S.	—	—	—	—	f.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Punctaria plantaginea</i> Grev.	Sp.	—	—	—	—	—
	S.	—	—	—	—	f.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>P. tenuissima</i> Grev.	Sp.	—	—	—	—	—
	S.	—	—	—	—	f.
	A.	—	—	—	—	—
	W.	—	—	—	—	—
<i>Pylaiella littoralis</i> Kjellm.	Sp.	o.	—	f.	o.	—
	S.	—	—	f.	o.	—
	A.	—	—	f.	o.	—
	W.	—	—	f.	—	—

Table VII (contd.)

Species	Season	Level			
		+ 5 to + 3 ft.	+ 3 to 0 ft.	0 to - 3 ft.	- 3 to - 5 ft.
<i>Rhodomela subfusca</i> Ag.	Sp.	—	—	—	f.
	S.	—	—	—	o.
	A.	—	—	—	o.
	W.	—	—	o.	o.
<i>Scytosiphon lomentarius</i> J. Ag.	Sp.	—	—	o.	—
	S.	—	—	—	f.
	A.	—	—	—	—
	W.	—	—	—	—
<i>Ulva lactuca</i> L. var. <i>latissima</i> DC.	Sp.	—	—	—	f.
	S.	—	—	—	f.
	A.	—	—	f.	f.
	W.	—	f.	f.	f.

Where fresh water has access to sandy pools it alters the vegetation considerably. This was observed in a few large pools which occur on the upper levels at the extreme north-eastern part of the survey area. In these pools the following species, which belong chiefly to the Chlorophyceae, are conspicuous:

<i>Chaetomorpha aerea</i> (whole year)	<i>Ectocarpus confervoides</i> (S.)
<i>C. tortuosa</i> (S.)	<i>Enteromorpha intestinalis</i> (whole year)
<i>Cladophora rupestris</i> (whole year)	<i>Monostroma Grevillei</i> (Sp.)
<i>C. sericea</i> (Sp. and S.)	<i>Percursaria percursea</i> (S.)
<i>Dumontia incrassata</i> (Sp. and S.)	<i>Rhizoclonium implexum</i> (Sp. and S.)

Q. *Laminaria saccharina* community.

Laminaria saccharina grows abundantly in the sublittoral region a few feet below L.W.S.T. level. At this depth the bottom is strewn with pebbles and boulders. This region was examined from a boat and samples of the vegetation were obtained by dredging. The *L. saccharina* plants are well developed and are attached to boulders and stones. Many of the other species found in this region are the same as those in the sand-pools on the lowest part of the shore and include the following:

<i>Aerochaetium Battersianum</i>	<i>Myrionema Corunnae</i>
<i>Ahnfeldtia plicata</i>	<i>Nitophyllum punctatum</i>
<i>Ceramium rubrum</i>	<i>Odonthalia dentata</i>
<i>Chorda filum</i>	<i>Phycodrys rubens</i>
<i>Chylocladia kaliformis</i>	<i>Phyllophora membranifolia</i>
<i>Cutleria multifida</i>	<i>Polysiphonia Brodiaei</i> var. <i>typica</i>
<i>Cystoclonium purpureum</i>	<i>P. elongata</i>
<i>Delesseria alata</i>	<i>P. urceolata</i>
<i>D. hypoglossum</i>	<i>Porphyra leucosticta</i>
<i>D. sanguinea</i>	<i>P. umbilicalis</i> var. <i>lacinata</i>
<i>Desmarestia aculeata</i>	<i>Porphyropsis coccineum</i>
<i>Dictyosiphon foeniculaceus</i>	<i>Ptilota plumosa</i>
<i>Ectocarpus siliculosus</i>	<i>Punctaria plantaginea</i>
<i>Enteromorpha Linza</i> var. <i>lanceolata</i>	<i>P. tenuissima</i>
<i>Halidrys siliquosa</i>	<i>Rhodomela subfusca</i>
<i>Laminaria saccharina</i>	<i>Rhodymenia palmata</i>
<i>Litosiphon filiformis</i>	<i>Sphaelaria bipinnata</i>
<i>L. pusillus</i>	<i>S. cirrhosa</i> var. <i>pennata</i>
<i>Lomentaria clavellosa</i>	<i>Ulva lactuca</i> var. <i>latissima</i>

This truly sublittoral community was not found in the corresponding position at Castletown Bay, but a community having a similar facies, "the

sublittoral community on pebbles", occurs at a higher level between low-water mark of neap and spring tides at the extreme northern part of the survey area at Castletown Bay.

COMPARISON WITH CASTLETOWN BAY, I.O.M.

When the survey areas of north Cumbræ and Castletown Bay are compared it is found that the majority of the algal communities are common to both places. In many cases, however, the communities differ considerably in their extent and floristic composition, and the main points of difference may now be summarized.

The *Porphyra-Urospora-Ulothrix* community is remarkably well developed in the southern part of the Castletown Bay area where a clear zonation of the species occurs. Its development is not nearly so good at Cumbræ and no zonation of the species is apparent.

Of the *Laurencia* community, only a few small examples occur at Cumbræ, but at Castletown Bay the community is extensive and *Lomentaria articulata* is co-dominant with *Laurencia*.

The *Gigartina-Cladophora* community is common at Cumbræ but is not represented at Castletown Bay.

The *Enteromorpha Linza* community appears as small local developments at Cumbræ in contrast to a fairly extensive development at Castletown Bay, where *Cladophora arcta* and *Chordaria flagelliformis* are co-dominant.

The *Himanthalia* community, which is found in the southern part of the Castletown Bay area, is not developed in the Cumbræ area.

In the *Laminaria* community *L. Cloustoni* is sparse and poorly developed at Cumbræ but is abundant in the lower part of the community at Castletown Bay.

So far as pool vegetation is concerned, the majority of the pools at Castletown Bay are of the "coralline" type, whilst at Cumbræ sand-pools predominate.

Of the communities developed on sand, mud or pebbles, the following are found at Cumbræ but not at Castletown Bay:

- (1) *Pelvetia canaliculata* var. *coralloides* community.
- (2) *Chaetomorpha-Vaucheria* community.
- (3) *Rhodochorton* community.

The *Laminaria saccharina* community occurring a few feet below L.W.S.T. level at Cumbræ is represented in the Castletown Bay area by a community of a similar facies developed, however, at slightly higher levels.

CONCLUSION

The marine algal communities which occur at Cumbræ are those characteristic of sheltered shores. Of the sixteen which have been recognized eleven are restricted to rocky substrata while the remainder occur on sand, mud or

pebbles. The best developed communities of the area are the *Pelvetia-Fucus spiralis* community, the *Ascophyllum* community, the *Gigartina-Cladophora* community and the *Laminaria saccharina* community. The distribution of the several communities seems to depend mainly upon changes in the degree of slope of the shore. Where the slope is very gentle deposits of sand, mud and pebbles are formed, and in these situations the *Chaetomorpha-Vaucheria* and the *Rhodochorton* communities are particularly characteristic. On the rocky shore the *Pelvetia-Fucus spiralis*, the *Ascophyllum* and the *Fucus serratus* communities attain their best development where the slope is gentle. On the steepest rock surfaces, however, where there is considerable surf action, the *Gigartina-Cladophora* community predominates, and between the levels L.W.N.T. and M.S.L. it replaces the *Ascophyllum* and *Fucus serratus* communities. It is only on these steeper parts of the shore also that the "coralline" type of rock pool is found.

Comparison with the survey area at Castletown Bay shows that all but four of the north Cumbrae communities are represented in the former area, viz. the *Gigartina-Cladophora* community, the *Pelvetia canaliculata* var. *coralloides* community, the *Chaetomorpha-Vaucheria* community and the *Laminaria saccharina* community.

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REFERENCES

- Averages of Bright Sunshine for the British Isles.* M.O. 408, Air Ministry, 1936.
Averages of Temperature for the British Isles. M.O. 407, Air Ministry, 1936.
Baker, S. M. "On the brown seaweeds of the salt marsh." *J. Linn. Soc. (Bot.)*, **40**, 1912.
Baker, S. M. & Bohling, M. H. "On the brown seaweeds of the salt marsh." *J. Linn. Soc. (Bot.)*, **43**, 1915.
Börjesen, F. "The algae-vegetation of the Faeröese coasts." *Botany of the Faeröes*, **3**, 1905.
Cotton, A. D. "Clare Island survey. 15. Marine Algae." *Proc. R. Irish Acad.* **31**, 1912.
Gibb, D. C. "The marine algal communities of Castletown Bay, Isle of Man." *This JOURNAL*, **26**, 1938.
Jónsson, H. "The marine algae of Iceland." *Botany of Iceland*, **1**, Copenhagen, 1912.
Kylin, H. "Zur Kenntnis der Algenflora der norwegischen Westküste." *Ark. Bot.* **10**, Stockholm, 1910.
Mill, H. R. "The Clyde sea-area." *Trans. Roy. Soc. Edinb.* **36**, 1892.
Rees, T. K. "The marine algae of Lough Ine." *This JOURNAL*, **23**, 1935.
West Coast of Scotland Pilot, 1934.

NOTES ON A FENCING EXPERIMENT

BY TOM. M. HARRIS

IN July 1936 two 1 m. quadrats of mountain vegetation on Cader Idris, North Wales, were mapped and fenced against sheep. The quadrats are close to Llyn Aran at a height of about 500 m. In July 1938 they were mapped again.

Both were types of vegetation widespread in north Wales. One, on a gravelly and stony soil at the base of an old scree slope, was a mossy turf 1-2 cm. high consisting largely of diminutive plants of *Vaccinium myrtillus*, several widespread mosses and *Cladonia sylvatica* which together with a few small dicotyledons and a very little grass made up the ground cover. A minute plant of *Calluna vulgaris* was present; just here this species is uncommon. The most striking feature was the presence of shoots of *Lycopodium alpinum* and *L. clavatum*, which in marked contrast with the other vascular plants were of normal size and growing vigorously above the stunted turf.

After two years the change was striking. The enclosed vegetation was now a *Vaccinium* heath 10 cm. high with a few fairly tall grasses (*Agrostis vulgaris*, *Festuca ovina*, *Deschampsia flexuosa*) and a healthy young bush of *Calluna*, the only one obvious in the immediate neighbourhood. On the other hand, the mosses and lichens were almost all dead and the *Lycopodium* doing badly.

The other vegetation, on rather deep peat, consisted of the very prevalent *Juncus squarrosus*-*Nardus stricta* grassland. The rosettes of these two formed almost the whole ground cover, but in the ridges where the leaves of different rosettes met a good many species occurred partly covered by the leaves of *Juncus* and *Nardus* and all in a very ill-developed condition.

After two years the vegetation had altered greatly. The two original dominants were largely overgrown by a mixture of the plants originally confined to the margins. *Deschampsia flexuosa* was now doing well and so was *Vaccinium myrtillus*, while some bushy plants of *Empetrum nigrum* appeared to be encroaching on the other species.

Although the exclusion of grazing animals—that is, sheep, since these alone appear to be present—is not the only effect of the fencing, it appears that it might be the only factor of importance in causing this change. These results suggest that both of these very prevalent sorts of vegetation are determined largely by grazing, not to say overgrazing, by sheep, and that the species which dominate this vegetation are simply those plants the sheep avoid. The relative luxuriance of the enclosed vegetation and the greater representation of edible species even suggests that the mountain side might be more productive if grazed at long intervals only instead of being farmed as at present.

This work was carried out by two parties of Reading students as part of their Botanical training, and it is hoped that further observations will be made on these and other fenced quadrats which have now been set up.

THE EARLY GROWTH OF BEECH SEEDLINGS UNDER NATURAL AND EXPERIMENTAL CONDITIONS

By J. L. HARLEY

1. INTRODUCTION

In a previous paper (1937) the root system of adult trees of *Fagus sylvatica*, growing on three main types of soil, was briefly described. It was pointed out that although variations in vigour could be correlated with the types and states of mycorrhizal infection described, no elucidation of the significance of that infection could be obtained. It was considered desirable, therefore, to study the growth of seedlings on the same range of soil types, for two reasons. First, previous workers have shown that beech regenerates itself with the greatest difficulty, especially on poor soils, and therefore the seedling stage may be a particularly interesting and critical phase. Secondly, the seedling is the only stage in the life of the beech when the whole organism can be handled easily, for measurement and analysis.

It must be made quite clear at the outset, that the internal physiological conditions of the seedling, its habitat, and its relation to the habitat are all extremely different from those of adult trees under woodland conditions. Results obtained from the study of seedlings are therefore only applicable to the elucidation of problems concerning the adult tree in a very limited degree.

2. METHODS

Seedlings growing in woodlands under natural conditions, and in pots in the Botanic Gardens at Oxford, were kept under observation from the time of germination. The growth of root and shoot in length, fresh weight and dry weight were recorded at intervals. Nitrogen estimations were used as measures of mobilization of stores and of absorption from the soil. Later, several experiments were set up to elucidate specific points in the work.

Throughout the whole work the scarcity of woodland seedlings was a great handicap. The years 1933 and 1934 were both partial mast years, but in each case seedling mortality was very high on account of the dry weather in June and July of the following years. In 1934 late frosts in May also caused death. A small percentage of the seedlings of 1933 survived until the autumn of 1935. Nevertheless, the seedlings were sampled as completely as possible in the two years, and the observations have been treated statistically where possible.

The seedlings first appeared above ground in the latter part of April, and the first samples were taken from the woods in early May. In May and June

it was possible to sample them by throwing a missile and taking the nearest seedling to its landing place. Later, when drought had begun, this was impossible and seedlings had to be taken where found.

The records obtained by this method of sampling only yield data concerning those seedlings which remain living at each visit; that is, the population may vary in nature by the death, perhaps, of some whole variants. For instance, it is likely that seedlings of constantly damp soil will form a larger fraction of the whole population after very dry weather.

Woodland seedlings were sampled from two types of soil, which may be said to approach the extremes of the soil range of beech as a dominant tree.

The first was soil from the chalk escarpment of the Chiltern Hills. It has a high calcium carbonate content, high exchangeable calcium, high carbon and high nitrogen content, but a low carbon/nitrogen ratio. It is characterized also by rapid decomposition of debris falling upon it, and a large active population of both bacteria and fungi. Here the nitrate content is not only great but increases greatly on incubation. It will be referred to as the Escarpment Soil.

The second type was very acid soil of pH 4.2–4.8 with a tendency to podsol formation, found on the plateau of the Chilterns. It had no calcium carbonate, little exchangeable calcium, high carbon and low nitrogen content, and a high carbon/nitrogen ratio. The number of bacteria was small and the fungi moderately numerous. Little nitrate was present, and no increase was found after incubation. It will be referred to as the Plateau Soil.

A third soil from a single area was sampled. This was well illuminated and free from thick undergrowth, and may be compared with the larger more wooded areas which were sampled more completely. This soil, though low in total nitrogen content, had a moderately large bacterial and fungal population and a low carbon/nitrogen ratio. Nitrate was readily formed on incubation.

3. METHOD OF ESTIMATING TOTAL NITROGEN IN SEEDLINGS

The material which had been used for the estimation of total dry weight was preserved dry until it was convenient to analyse it.

The dry material was then subjected to a Kjeldahl digestion with concentrated sulphuric acid, potassium sulphate and copper sulphate. The clear liquid so obtained was diluted to a convenient volume, and an aliquot taken for ammonia estimation.

Ammonia was estimated by the method of Chibnall and Westall which is a modification of the Parnas-Heller distillation for use with reduced pressure. The aliquot is placed in the distillation flask, made alkaline, and distilled under reduced pressure (*ca.* 2 cm.) into standard 0.01N H_2SO_4 , the excess of which is back-titrated with 0.01N CO_2 -free NaOH in the presence of methyl red.

4. GENERAL DESCRIPTION OF WOODLAND SEEDLINGS

After germination in April, the seedlings grew rapidly, and by the end of May the majority had produced two leaves. The tap-root with a few simple branches penetrated downwards through the leaf litter towards the soil. During June, if the roots had reached the mineral soil, infection by mycorrhizal fungi took place.

In all cases the tap-root comprised the greater part of the root system. This bore a variable number of laterals, the short sublaterals of which were, in the majority of examples, infected. Infection was less complete in escarpment soils. Frequently, especially in plateau soil, seedlings failed to reach the mineral layer because of the depth of leaf litter. These seedlings usually remained uninfected, and died during the drought. Similarly, seedlings which failed to penetrate the mineral soil because of its compactness, had a poorly developed or deformed root system and also did not survive.

The main variations in the nature of the two populations were apparent from general observation. First, in the escarpments, the onset of dry weather in the early summer caused general death and early fall of cotyledons. In plateau soil dry weather caused death of those seedlings that had failed to reach the mineral layer. Those remaining were of two types; seedlings that were enabled to penetrate through the leaf-litter, owing, apparently, to good light conditions that produced strong growth, and those germinated in places where the leaf-litter was not too deep. Secondly, it was apparent that the seedlings in the escarpment at the end of two years were in general well distributed through the woods. Those of plateau soil became in the second year almost restricted to the lighter parts of the woods and were usually fewer in number.

5. THE GROWTH OF SEEDLINGS ON ESCARPMENT AND PLATEAU SOILS

The numerical data for seedlings on these soils are fairly complete, and from them a comparison of seedling growth on the extremes of the range of soil studied can be obtained. Tables I and II give mean values of the measurements made at various times in the two seasons.

Both populations were characterized by an initial rapid increase in height, followed, in the escarpment soil, by an irregularly level phase, and in plateau soil by a gradually increasing phase.

Similarly, the growth of roots was rapid at first but became slower later. This slowing may have been in part an artefact. In plateau soil there was an actual diminution in root length in the four successive samples from May till September. It may be shown by comparing the means of September and May, by Fisher's "*t*" test, that the probability that these means are really different is 20 to 1. Hence the fall in length was probably real. It may be ascribed to the high mortality of those seedlings germinating in deep litter. This forms, as

Table I. *Escarpment seedlings (means of measurements)*

Measurement	June	July	Sept.	Sept. 2nd year
Height, mm.	109.6	104.0	101.5	129.0
Root length, mm.	80.8	74.0	74.0	84.0
Shoot weight, g.	0.58	0.33	0.32	0.39
Root weight, g.	0.15	0.10	0.12	0.23
No. of leaves	2.0	2.2	2.3	3.6
Shoot dry weight, g. $\times 10$	1.1972	1.1709	1.6173	1.9052
Root dry weight, g. $\times 10$	0.2414	0.3018	0.4119	0.9200
Total nitrogen, mg.	5.38	3.48	3.77	3.51
Shoot nitrogen, mg.	4.66	2.78	2.90	2.62
Root nitrogen, mg.	0.72	0.70	0.87	0.89
Water % of dry wt. in shoot	383	175	100	105
Water % of dry wt. in root	520	230	190	150

Table II. *Plateau soil seedlings (means of measurements)*

Measurement	May	June	July	Sept.	Sept. 2nd year
Height, mm.	56.8	94.3	107.8	126.5	146.3
Root length, mm.	87.2	83.9	79.3	71.5	84.1
Shoot weight, g.	0.46	0.50	0.43	0.33	0.62
Root weight, g.	0.09	0.16	0.13	0.16	0.44
No. of leaves	0.0	1.8	2.0	2.0	5.6
Dry weight of shoot, g. $\times 10$	0.7054	0.9782	1.1781	1.9291	3.0236
Dry weight of root, g. $\times 10$	0.0337	0.3324	0.2949	0.8066	1.8686
Total nitrogen, mg.	4.11	4.01	4.00	3.61	4.82
Shoot nitrogen, mg.	3.67	3.30	3.23	2.51	3.46
Root nitrogen, mg.	0.44	0.71	0.77	1.11	1.36
Water % of dry wt. in shoot	557	400	258	73	106
Water % of dry wt. in root	2570.6	380	350	100	140

Watt (1923), Barrett (1931) and Somerville (1893) have pointed out, and as has been mentioned above, a good matrix for germination but a poor one for survival, owing to its low water-retaining capacity. It appears, therefore, that there may have been two factors in operation in the plateau soils, a differential mortality of long-rooted seedlings, and a real slowing of root growth, producing together the appearance of a fall in root growth.

The fresh weights of both populations during the first year show a phase of rapid increase in weight of the tops followed by a fall, and a roughly level phase in the roots. In the second year there was in each case an increase in the fresh weights of both roots and shoots.

The main irregularities of the fresh-weight figures are explicable from a consideration of the figures for dry weights and water contents. The water content of both root and shoot, in both soils, decreased very rapidly throughout the first year, and arrived at low values in September. The shoots contained 100 and 73% water of dry weight, and the roots 150 and 100% in escarpment and plateau soils respectively. At the end of the second year the water content was of the same order. The fluctuating values of fresh weight were therefore due *in part* to the decreasing water content combined with a generally increasing dry weight.

The higher values of water content in the escarpment in September are surprising because the soil appeared to dry out more rapidly than on the

plateau. This is reflected in the very much lower water content of seedlings on this soil in July. The water content of seedling, however, is not necessarily a true indication of the water conditions in the soil, since it fluctuates with age and nutrition under controlled conditions.

The total nitrogen contents of seedlings and of roots and shoots are given as mean values obtained by analysis of samples in groups of ten (Tables I and II). (Note that this is total nitrogen per seedling and not referred to any weight basis.)

In each case the total nitrogen per seedling was less at the end of the first year, before the final leaf fall, than on germination. This was associated with the fall of the cotyledons. The fall was sudden and widespread in seedlings of the escarpment soils, and occurred in June and July. The loss on plateau soils was not so great and occurred later. It is important to note that the final total nitrogen content at the end of the first year was similar in the two types of seedling. The escarpment seedlings seemed to start life with greater reserves in their cotyledons and lose more than did the seedlings of plateau soils.

There was an increase of nitrogen in the roots due to translocation from the shoots in the first year. This was more rapid in the early part of the season and became slower later.

During the second year there was apparently some absorption from the soil among the seedlings of plateau soil, as shown by the increased total nitrogen. There was no apparent absorption in the escarpment seedlings over this period. Thus, in the latter soil, the population of seedlings existing at the end of two seasons' growth had a smaller mean total nitrogen content than that which survived on plateau soil. This may have been a reflection of the differential mortality recorded above, leading, in very acid soils, to the survival of those seedlings growing in good light conditions.

6. COMPARISON OF SEEDLINGS GROWING ON VERY WET SOIL WITH THOSE FROM NORMAL SOIL

In autumn 1934, certain of the seedlings from plateau soil were found in very wet pockets of soil. These had very little mycorrhizal infection. They have been compared with a sample of seedlings found under more normal conditions near-by. The comparison so made brings out the effect of excess water in the soil, upon mycorrhizal infection and upon growth. The data are summarized in Table III. From this it seems that there was no significant difference between the means in fresh weight of either shoot or root. The seedlings of wet soil were however, taller and possessed larger roots with greater numbers of laterals of the first order.

The total nitrogen and the nitrogen of shoot and root show that both the normal seedlings and the seedlings of wet soil were similarly affected by factors changing the rate of mobilization and causing a loss of nitrogen.

The slight differences that existed between the samples might have been due either to lack of infection, to the wetness of the soil, or to absence of root competition in very wet soil which is poorly exploited by the roots of adult beech trees.

Table III. *Means of measurements*

	Wet soil	Normal	Significance by <i>t</i> test
Leaves present	1.4	1.6	Insig.
Leaves set	2.3	2.2	Insig.
Shoot fresh weight, g.	0.29	0.37	Insig.
Root fresh weight, g.	0.13	0.17	Insig.
Height, mm.	151	120	Sig. ($P < 0.02$)
Root length, mm.	110	70	—*
Total nitrogen, mg.	3.64	3.58	—
Nitrogen per shoot, mg.	2.41	2.50	—
Nitrogen per root, mg.	1.23	1.08	—
Infection	Very slight	Fairly complete	
Root branches of the first order	68	45	Sig. ($P < 0.01$)
Root branches per cm.	4.5	3.75	—

* The difference between the means here was possibly significant, but, owing to the loss of the individual measurements, cannot be calculated.

7. THE SEEDLINGS OF THE BETTER LIGHTED CLEARING

The following data were obtained from seedlings in one clearing which was open to light from the north and south. The direct sunlight from the west was partially, and that from the east wholly, cut off.

A study of Table IV will show that the growth in root length was greater during the first year than that on the other two types of soil studied. Both the height and root length were greater after two years' growth, and larger numbers of leaves were produced. No differential mortality of seedlings was observed, so the means may be taken to describe the condition of the whole population.

Table IV. *Seedlings of the clearing (means of measurements)*

Measurement	June	July	Aug.	Sept.	Oct.	Sept. 2nd year
Height, mm.	102.0	92.4	109.0	104.5	155.0	177.5
Root length, mm.	75.3	60.4	91.3	112.5	110.2	134.0
No. of leaves	2.3	—	—	2.5	1.9	4.4
Shoot fresh weight, g.	—	—	—	0.44	0.74	—
Root fresh weight, g.	—	—	—	0.34	0.70	—
Shoot dry weight, g. $\times 10$	—	—	—	—	—	2.8757
Root dry weight, g. $\times 10$	—	—	—	—	—	2.7521
Total nitrogen, mg. per seedling	4.91	—	—	4.53	3.96	5.44
Shoot nitrogen, mg. per seedling	—	—	—	3.17	2.37	3.25
Root nitrogen, mg. per seedling	—	—	—	1.36	1.59	2.19

The estimates of nitrogen content of seedlings show that, as in the other types, there was a loss of total nitrogen up to September in the first year. This may be attributed to loss of cotyledons. In October of the first year a further loss was observed, coincident with the loss of leaves. However, absorption in the second year brought the total up to a value higher than that obtained at the first analysis of the first year.

A calculation of root/shoot dry weight ratio at the end of the second year shows that in these seedlings the ratio approached unity, whereas in the seedlings of the escarpment it was 0.48, and in those of plateau soil 0.62.

The factors that might have contributed to these differences are to be sought among the following:

- (1) Soil type.
- (2) Increased light intensity.
- (3) Small root competition in the clearing.

It seems improbable that relative degrees of infection played a part here, since it was found that the root systems of these seedlings were infected to a similar extent by mycorrhizal fungi as the seedlings from the plateau soils described above. The seedlings of the escarpment, on the other hand, were frequently infected to a smaller extent than either.

The similarities between all woodland seedlings, especially in the loss of nitrogen in the first year, is striking, and a comparison with plants grown in pots is most instructive.

8. SEEDLINGS GROWN IN POTS

Seedlings were raised in light garden soil¹ in pots under full sunlight, and kept watered in dry weather. A small amount of beech humus was added to each pot in an attempt to secure the presence of the mycorrhiza fungi.

The experiment was started in early May and growth was very rapid. At the end of June an extensive root system had been produced, occasionally involving branches of the fourth order. These were not found to be infected by this date. The whole crop was harvested in August, and a careful examination showed that there were a few infected roots on the majority of the seedlings. These mycorrhizas were very small in size, and the greater part of the root systems were uninfected, except for epiphytic hyphae on the surface of the roots.

Measurements of the heights and lengths of the roots were taken, and total nitrogen was estimated on a sample. Table V gives a comparison of these seedlings with those obtained from the moderately acid soil at the end of the second year of growth.

A comparison of these means shows that the amount of growth made by the potted seedlings between May and August of one year was of the same

Table V

Origin of seedlings	No. of leaves set	Height mm.	Length of root mm.	Total N per seedling mg.
Pots 1 Aug. of 1st year	6.5	155.7	193.7	10.7
Moderately acid soil, in Sept. of 2nd year	6.8	177.5	134.0	5.44

¹ Analysis of the soil performed later showed it to be slightly calcareous, of moderately high nitrogen content, with a low carbon-nitrogen ratio, and rapid nitrate-forming capacity.

order as that made by the woodland seedlings in two growing seasons. Moreover, it seems certain that the root growth and the absorption of nitrogen of the seedlings from the pots were very much greater than that of the woodland seedlings.

The factors contributing to the differences between these seedlings may be among the following (for potted seedlings):

- (1) Increased light intensity.
- (2) Different soil.
- (3) Abundant water supply.
- (4) The absence of root competition.
- (5) The absence of extensive infection.

Of these factors, low light intensity and extensive root competition seem to be always present in the beechwoods sampled, whereas soil constitution, water, and extent of infection may vary more from one situation to another. The general similarity of all seedlings from all types of wood, together with the sharp differences between them and the seedlings from the pots, leads one to suppose that one or both of the first-mentioned factors may be very important in its effect on seedling growth under natural conditions.

This hypothesis was tested in the following experiments.

9. POT EXPERIMENTS

Experiment 1

First a simple transplant experiment was performed. This involved the removal of ungerminated seeds and soil from a wood, and allowing the seeds to germinate under full light intensity and in the absence of root competition.

In the middle of July these were harvested and compared with seedlings growing naturally in the same place, under the canopy, where the seeds were obtained.

The results are given in Table VI. Insignificantly larger numbers of leaves were set and retained by the transplanted seedlings. In height, again, no significant difference was produced by the treatments, but the shoots of woodland seedlings had greater fresh weight.

The roots of the transplanted seedlings were greater in length and fresh weight.

The dry-weight data show that the transplanted seedlings were much heavier both in root and shoot. The dry weight of the roots of the transplanted seedlings was about treble that of the woodland seedlings. Moreover, the root/shoot dry-weight ratio of the transplanted seedlings was 0.52 whereas that of the woodland seedlings was 0.23.

The total nitrogen content of the seedlings was identical in the two treatments (within the bounds of experimental error), 4.08 and 4.09 mg. per seedling for woodland and transplanted seedlings respectively. There was, however,

Table VI. *Experiment 1 (means of measurements)*

Measurement	Woodland seedlings	Potted seedlings	Increase or decrease due to treatment	Significance of difference between means
Leaves set	3.0	3.3 3.7 } 3.5	+ 0.5	Insig.
Leaves present	2.7	3.3 2.7 } 3.0	+ 0.3	Insig.
Height, cm.	11.0	10.4 11.0 } 10.7	- 0.3	Insig.
Root length, cm.	6.0	8.2 7.0 } 7.6	+ 1.6	Sig. ($P < 0.01$)
Shoot fresh weight, g.	0.45	0.36 0.35 } 0.36	- 0.09	Sig. ($P < 0.01$)
Root fresh weight, g.	0.12	0.29 0.30 } 0.30	+ 0.18	Sig. ($P < 0.01$)
Shoot dry weight, g.	0.1173	0.1902 0.1877 } 0.1889	+ 0.0716	-
Root dry weight, g.	0.0271	0.0980 0.0963 } 0.0972	+ 0.0701	-
Water % dry weight of shoot	275	84 90 } 87	- 188	-
Water % dry weight of root	300	190 200 } 195	- 105	-
N in shoot, mg.	3.44	2.74 2.70 } 2.72	- 0.72	-
N in root, mg.	0.64	1.39 1.35 } 1.37	+ 0.73	-
N in shoot % of total N	84.4	66.6 66.2 } 66.4	- 18.0	-
N in root % of total N	15.6	33.4 33.8 } 33.6	+ 18.0	-

double the amount of nitrogen in the roots of the transplanted seedlings than there was in the roots of the woodland plants.

Table VII gives the nitrogen content of the cotyledons of similar seedlings taken two weeks later:

Table VII

Origin of seedlings	No. of cotyledons in sample	N per seedling in cotyledons mg.	N in cotyledons % of initial seedling N
Woodland	22	2.46	61.5
Woodland	22	2.42	60.5
Pots	10	0.95	23.7

It is clear from these results that nitrogen was removed from the cotyledons of well-lighted seedlings grown in pots to a much greater extent than from those of shaded woodland seedlings during this period of growth.

There seems no doubt that increased light intensity promotes seedling growth and the mobilization of stores. The characteristic in which shaded seedlings were larger, that is fresh weight of shoots, was the result of the greater water content of shaded plants and may be a reflexion of abnormal metabolism as well as decreased evaporation rate under the canopy, and is perhaps the reverse of what would be expected if root competition were a factor limiting growth.

This experiment may be criticized on the ground that the normal woodland seedlings provided an incomplete control. It must be made clear that the abnormal exposure of the seedlings in the pots to frost and to extreme desiccation would be expected to exert influences opposite to those due to the increased light intensity and decreased root competition.

To provide more definite information further experiments were designed.

Experiment 2

Two sets of boxes containing a compost of beech humus and sand were set in the open and allowed to weather. They were then planted with seedlings in the cotyledon stage from a wood on plateau soil in early May.

One set of boxes was shaded with sacking, which cut off about 90% of the light, as measured with an Avo photometer. The other set was covered with muslin which only reduced the light by 5% of direct sunlight, but afforded some protection from late frosts and drying winds.

The seedlings were watered once a week in dry weather.

On 21 September these were harvested, measured, weighed and analysed. The results are given in Table VIII.

In these plants, harvested two months later than those in Exp. 1, growth was significantly greater in light than in shade. Not only were the heights of lighted seedlings greater, but also the fresh weights, which were greater in the woodland seedlings in the last experiment. This latter may have been due to these seedlings being more mature. The water content of both root and shoot was, nevertheless, greater in the shaded seedlings.

Here again, the root/shoot dry-weight ratio was increased from 0.44 to 0.98 by the removal of shade, and here it seems to be brought about by the effect of light only.

The nitrogen content of both shoots and roots was greater in the light.

The mean initial total nitrogen was 4.02 mg. per seedling. Hence there was slight absorption in the shaded seedlings up to a value of 4.73 mg. per seedling, while the lighted seedlings increased their nitrogen content by 100% to 8.12 mg. per seedling.

Here again more variables were introduced than have been considered in the experiment. Although time was allowed for weathering of the compost before planting and shading, further release of nitrogenous material may have taken place in the light (Glømme and Hesslemann). Moreover, the large root systems of the lighted seedlings were infected to a greater extent than the darkened seedlings, although infection, taken as a whole, was not as great as was expected. The limitation of the darkened seedlings may be the outcome of both direct and indirect retardation of processes under these conditions.

Although there appears to be a definite retardation of the seedlings in the shade, which may be ascribed to an effect of diminished light, it is important to note that these seedlings are larger than any of those obtained from woods at

leaves set to leaves retained was 1·2, whereas in Exps. 1 and 2 it was 1·1 in the shade and 1·2 in the light. The great loss of leaves in the light treatment of this experiment, giving a ratio of 9·4, is due to the effect of increased light acting in conjunction with the nature of the soil. The suggestion that it might be ascribed to nitrogen starvation does not seem probable for two reasons. First, the nitrogen content per unit dry weight of the roots is 9·7 mg. per g. here, whereas it was only 6·6 mg. per g. in the roots of the light treatment of Exp. 2. Secondly, in other experiments not described here, a similar compost to which nitrate was added was used for growing seedlings from the same sample of seed. These also showed early fall of leaves in the light although they were well supplied with nitrogen. Certain experiments still in progress with older seedlings indicate that three natural soils all poor in available calcium bear seedlings whose leaves fall earlier than three calcium-rich soils, in full sunlight. The explanation may therefore lie in the base content of the compost.

These losses would affect the dry-weight estimations greatly, so that dry weights of roots and stems were estimated instead of dry weights of root and shoot.

The height of the shaded seedlings was greater than that of the lighted seedlings, but there was no difference in length of the roots. The dry weight of the lighted seedlings seemed to be greater in both root and stem.

The root/shoot ratio by dry weight cannot be of value here owing to the loss of leaves, nevertheless a root/stem ratio shows that the unshaded seedlings had a value 1·57 which is higher than that of the shaded seedlings 1·29.

The nitrogen of the roots was greater, and that of the stems insignificantly greater in lighted seedlings. Owing to the loss of the leaves the total nitrogen of the latter plants was less than that of their controls.

It is noticeable that these seedlings raised in a soil poor in nitrogen were larger than seedlings from woodlands. This may be ascribed to the higher light intensity, to which both sets were subjected. The stores of nitrogen in the cotyledons were utilized to a greater extent in the production of a larger body, but a net loss of nitrogen was sustained in both sets.

An interesting comparison may be made between the lighted seedlings of Exps. 2 and 3. These were derived from the same seed planted at the same time, by the same methods and harvested within a day of one another. The soils constitute the sole intentional difference between the treatments.

The outstanding differences in growth were: the fewer leaves produced in the sawdust compost, their earlier fall, smaller height and length of roots, very much smaller dry weight of roots, smaller total nitrogen per unit root, and greater nitrogen per cent dry weight of roots.

The presence of mycorrhiza fungi was assured in each case by inoculation with beech humus, but in neither case was infection as complete as it is under natural conditions on acid soil. The seedlings of the sawdust compost were somewhat less infected than the others. Without more complete data on this

point it is therefore not possible to ascribe the differences between the treatments to direct influence of soil alone. Nevertheless, factors arising out of the soil are in some way responsible for the differences.

These experiments therefore indicate definitely the immense importance of light intensity under woodland conditions, and also show that the complications arising out of soil composition and structure are of secondary importance at this stage of the life of the beech.

10. DISCUSSION

In these experiments it appears that shading of seedlings produces symptoms similar to those found in seedlings under woodland conditions. These are:

- (1) Great water content.
- (2) Poor root growth.
- (3) Low dry weight of both root and shoot.
- (4) Low root/shoot ratio (by dry weight).
- (5) Incomplete mobilization of nitrogen before the fall of the cotyledons.
- (6) A very small or complete lack of absorption of nitrogen.

These symptoms have frequently been associated with reduced light intensity. Shirley (1929*a, b*) found that the dry weight of oaks was proportional to light intensity up to 20% of full summer light, but that thereafter there was no direct proportionality. He also reported a depression of root/shoot ratio in low light intensities. Holch (1931), working with seedlings of deciduous trees, found that growth was proportional to photosynthetic activity, and, given adequate water, was greatest in full light. The depression of root/shoot ratio in shade conditions was stressed by Aldrich-Blake (1932) in the case of forest-tree seedlings, and by Crist & Stout (1929) for certain herbaceous plants.

On the other hand, Burger (1930) showed that the roots of forest trees, including beech, were better developed in poor soils than in rich ones, and made up a greater proportion of the dry weight of the plant.

In this present work it seems probable that any increased root/shoot ratio in seedlings of the plateau soils, which might have been expected on the basis of Burger's work, was removed or masked by limitations produced by other factors, such as low light intensity.

The work of Krauss & Kraybill (1918), and later that of Reid (1926), shows very plainly that low carbon/nitrogen ratios in tomato are associated with weak growth. Moreover, Reid showed that low carbon content, associated with normal nitrogen supply, caused increased succulence and poor root growth. These abnormalities might be overcome by increased photosynthesis.

The symptoms described above are not apparent in those beech seedlings grown in full light. It therefore seems probable that the seedlings under natural conditions are subject to a light factor which limits growth. This is in agreement with Watt, who considered that light was an important factor in the

regeneration of beechwoods. Gordon (1912), however, suggested that light intensity of about one-fortieth of full daylight was optimum for "advance growth" of sapling beech. The shading in Exp. 3 of the present work was such as shut off two-fifths of full daylight, and even this shade seemed to cause some slowing of growth in young seedlings except height growth which was slightly increased.

There is, however, a body of opinion which suggests that light does not play an overwhelmingly important part in forest regeneration. Fricke (1904) came to the conclusion, by means of trenching experiments with seedlings, that root competition was the main factor limiting regeneration in the case of beech and other trees. Bates (1925), and later Bates & Roeser (1928), showed that low light intensities decreased the root branching of conifers, and might often lead to their succumbing to poor soil conditions, but on the whole they suggested that light was rarely limiting under natural conditions. In their laboratory work they showed that only the largest and heaviest seedlings survived in the weakest light.

A further view is held by Aaltonen (1926) and Grasowski (1929) that in their observations light was not so important an influence on growth as root competition.

Although from these present observations and experiments there is no doubt that light intensity exerts the dominating influence on growth, there are several indications that complicating factors may be present. It has been noted that in acid plateau soils there is a tendency for survival of only those seedlings that germinate in the better lighted situations. There is reason to believe, however, that this is not necessarily due to the additive effect of soil and light such as Bates observed, but due rather to the harmful accumulation of leaf-litter in these more shaded situations. Watt (1923), Somerville (1895) and Barrett (1931) have all observed that leaf-litter is a good matrix for germination but a poor substrate for growth, owing to large fluctuations in moisture content. Therefore, one would expect only those seedlings of greatest vigour, such as are subjected to good light conditions, to survive in woods where litter accumulates to a great depth.

A further point relating to the complicating effect of soil upon light arises out of Exp. 3. Here, in a soil poor in nitrogen, early leaf fall is noted in the light. Although it has been pointed out that nitrogen starvation is not the cause of leaf fall here, the early loss of the leaves may be important in limiting the growth of the seedlings in size and weight.

The results of this investigation have important bearings on the problem of the mycorrhiza of beech. It would be expected that if infection had an important effect on the nutrition of the seedling, some factor other than light would have dominated growth. In fact one would have expected, that in poor soil at any rate, root competition would have been the main factor limiting growth.

The evidence against this is convincing. The water content of seedlings is not only higher under woodland conditions than in full sunlight and in the absence of root competition (Exp. 1), but also, and this is even more important, no significant differences are found between those seedlings from wet pockets in plateau soil and those from the surrounding drier soil where root competition with adult trees was more severe.

Root competition for nitrogen can be no handicap during the first year of seedling life. There is ample evidence that nitrogen is present in the cotyledons in excess of requirement for growth under woodland conditions during the first year, since mobilization of cotyledonary stores was very incomplete. A similar result was obtained in the shading experiments.

There remains the possibility that nitrogen supply may have been a factor influencing growth in the second year. To reach a decision here it is essential to consider the ratio of nitrogen to dry weight of the root systems of all the samples of seedlings obtained in the field. These are shown in Table X.

Table X. *Total nitrogen mg. per g. dry weight*

	May	June	July	Sept.	Sept. of 2nd year
Plateau soil	130.6	21.3	26.1	13.5	7.2
Well lighted clearing	—	—	—	—	7.9
Escarpment soil	—	29.8	23.2	21.1	9.6

It will be seen that the nitrogen per unit dry weight decreases in plateau and escarpment soils throughout the two years, reaching the low value of less than 10 mg. per g. The value for plateau soil is less than that for escarpment.

To decide whether this low value in plateau soil is due to nitrogen limitation, one can compare it with the values of nitrogen per unit dry weight of the roots of seedlings in the experiments.

Table XI

Exp.	Date of harvest	Root N, mg. per g. dry weight	
		Shade	Light
1	16 July	23.4	14.1
		—	14.0
2	21 Sept.	14.8	6.8
		14.7	6.3
3	20 Sept.	10.7	9.9
		11.1	9.4

It is at once apparent that the better grown lighted seedlings have a lower nitrogen/dry-weight ratio in their roots than their shaded controls. Moreover, this ratio is lower in the lighted seedlings of Exp. 2 than in any of the roots of woodland seedlings in their second year. The seedlings of Exp. 2 had absorbed nitrogen from the soil and showed no sign of nitrogen starvation.

One can conclude from these results that mycorrhizal infection plays a very limited part in the nitrogen nutrition of beech seedlings under natural conditions during their first two years of growth.

Further experiments are in progress which have been designed to elucidate the relation of mycorrhizal infection to nutrition in other conditions and later in life.

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REFERENCES

- Aaltonen, V. T. "The space arrangement of forest trees and root competition." *J. For.* **24**, 6, 1926.
- Aldrich-Blake, R. N. "The influence of nutrition on the relative root and shoot development of forest tree seedlings." *Forestry*, **6**, 40, 1932.
- Barrett, L. I. "The influence of forest litter on the germination and survival of forest oak, *Q. montana* Willd." *Ecology*, **11**, 476, 1931.
- Bates, C. G. "The relative light requirements of some conifer seedlings." *J. For.* **23**, 869, 1925.
- Bates, C. G. & Roesser, J. "Light intensities required for the growth of coniferous seedlings." *Amer. J. Bot.* **15**, 185, 1928.
- Burger, H. "Holzarten auf verschiedenen Bodenarten." *Mitt. Schweiz. Zent. Anst. forstl. Versuchsw.* **16**, 49, 1930.
- Chibnall, A. C. & Westall, R. O. "The estimation of glutamine." *Biochem. J.* **26**, 122, 1932.
- Crist, J. W. & Stout, G. S. "The relation between top and root size in herbaceous plants." *Plant. Physiol.* **4**, 63, 1929.
- Fricke, A. "Licht und Schattenholzarten." *Zbl. ges. Forstw.* **30**, 315, 1904.
- Glømmé, H. *Undersøkelser over ulike humustypers ammoniak-og nitratproduksjon sampt factorsomhar innflytelse- po disse prosesser.* 1932 (with English summary).
- Gordon, C. B. "On the relation of light intensity to advanced growth in oak and beech forests." *Trans. R. Scot. Arb. Soc.* **26**, 47, 1912.
- Grasowski, A. "Some aspects of light in the forest." *Yale For. Sch. Bull.* **23**, 1929.
- Harley, J. L. "Ecological observations on the mycorrhiza of beech" (preliminary note). *This JOURN.* **25**, 421, 1937.
- Hesselmann, H. *Studier over Barrskogens Humustake Dess Egenskaper och Beroende av Skogsvaden.* Stockholm, 1926 (with German summary).
- Holch, A. E. "Development of roots and shoots of certain deciduous tree seedlings in different forest sites." *Ecology*, **12**, 259, 1931.
- Krauss, E. J. & Kraybill, E. R. "Vegetative growth and reproduction with special reference to tomato." *Bull. Ore. Agric. Exp. Sta.* no. 149, 1918.
- Reid, M. E. "The growth of tomato cuttings in relation to stored carbohydrate and nitrogen compounds." *Amer. J. Bot.* **13**, 548, 1926.
- Reid, M. E. "The relation of the composition of seeds and the effects of light on the growth of seedlings." *Amer. J. Bot.* **16**, 747, 1929.
- Shirley, H. L. "The influence of light intensity and light quality on the growth of plants." *Amer. J. Bot.* **16**, 354, 1929a.
- Shirley, H. L. "Light requirements and silvicultural practice." *J. For.* **27**, 535, 1929b.
- Somerville, W. "The natural regeneration of woods." *Trans. R. Scot. Arb. Soc.* **13**, 63, 1893.
- Watt, A. S. "On the ecology of British beechwoods, with special reference to their regeneration." *This JOURN.* **11**, 1; **12**, 145 and **13**, 27, 1923-5.

A SYMPOSIUM ON THE RECIPROCAL RELATIONSHIP OF ECOLOGY AND TAXONOMY¹

1. INTRODUCTION

By A. G. TANSLEY

THE symposium that will occupy us to-day is somewhat of an experiment, but an experiment which I venture to think has good prospects of success. We owe its initiation very largely to active members of the Association for the Study of Systematics in relation to General Biology, which was formed in 1937 as a result of the widespread feeling that the study of the systematics of animals and plants was very much out of touch with biology at large. That Association counts among its members enthusiastic exponents of what may perhaps be called "The New Systematics" which seeks largely to supplement the traditional methods of the museum and the herbarium—always of course indispensable—by genetic analysis and by study of the behaviour and relations of species and varieties in the field. It is especially in this last province that the new systematist comes directly into contact with the ecologist. Both study living plants and animals in the field, though one has as his immediate aim the clarification of their classification, the other a knowledge of their life economy—in the case of plants, particularly, of their relations to one another, to the communities of which they form part and to their whole environment. But it may be held that the ideal new systematist cannot fully realize his aims unless he is also an ecologist, for the role of a species in vegetation is an essential part of its character, not to mention the fact that different conditions of life often modify the structural features on which the taxonomist must primarily depend. No one can really understand the structural features of species unless he knows their life histories, and the life history of a plant and its organs under various conditions is a large part of what is called its autecology. Nor can the ecologist dispense with a sound knowledge of recent advances in the taxonomy of species and varieties he deals with. In other words, he ought to know as accurately as possible the real nature and status of the constituent material of the vegetation he studies, or his descriptions and lists may be very misleading. There is no doubt, I think, that one and the same person really ought to work both at species and vegetation. As things are, what with divergences of primary interest and various professional pre-occupations, the systematist still tends to ignore the part actually played by

¹ The substance of seven papers under this general heading was given at the annual meeting of the British Ecological Society, the President, Prof. A. G. Tansley, F.R.S. in the chair, held at University College, London, on Friday, 6 January, 1939. A summary of the discussion which followed is also given.

species in the field, and the ecologist to be content with a dangerously sketchy knowledge of the species he cites. There has been notable improvement on both sides since I can remember, but there is still room for much more. These considerations will, however, doubtless be developed by subsequent speakers, and I will say no more about them now, except to reiterate that the more individual workers can follow both disciplines the better for the advancement of the science.

The speakers (three botanists and three zoologists) will each deal with a special aspect of the general topic, but since each is limited to 15 min. he will scarcely be able to do more than touch upon a few salient points. The promoters of the symposium particularly desire, after the symposiasts have finished, a good general discussion of the points raised and of any other points on the general subject that members of the Society or visitors think important. In that general discussion we hope as many members as possible will take part.

2. THE ECOLOGIST APPRECIATES AND CRITICIZES THE TAXONOMIST

By E. J. SALISBURY

ONE part of my task is a comparatively easy one, namely, to express the appreciation of the ecologist for the taxonomist's contribution towards his investigations.

The ecologist, if his work is to have permanent value, must distinguish precisely the organisms which he studies, moreover, since correlation between the work of different investigators is essential to progress, the meticulous identification and precise naming of the biological units with which he is concerned is an essential part of the ecologist's task.

No one would expect every ecologist to be an expert systematist but it is fundamental if the synthesis of results is to yield order and not chaos, that every ecologist should know accurately the plants and animals with which his studies are concerned. Taxonomy for the ecologist is not an end in itself, but it cannot be too strongly emphasized that an adequate acquaintance with taxonomy is an indispensable part of the ecologist's equipment.

The communities which comprise our vegetation units, of whatever status, are mostly characterized, it is true, by frequency differences with respect to the constituent species but, in addition, there are those more specialized types, which we designate characteristic or exclusive species, that are restricted in a more or less marked degree to one or more particular types of habitat. The study of the morphological segregation of these species, which play an all-important role in the floristic characterization of many plant communities, is of no less value than the study of their physiological requirements, since the

latter, which is the especial province of the ecologist, can only follow a precise identification of the material to be investigated.

How important is the systematist's contribution to ecological studies can perhaps be best realized when we recall that it is quite commonly the smaller and more critical of the systematic units, rather than the larger and more readily distinguished, which are of the greatest ecological significance. The aggregate species or Linneon may often have so wide a range of tolerance, so extended a distribution, as to present little interest from the point of view either of ecology or plant geography. Though we must not fall into the error of assuming that such wide range of tolerance, when exhibited by a segregate, is any less a specialization than adaptation to more restricted conditions.

Within the Linneon aggregate *Cirsium eriophorum* L. with its wide geographical range, there have been distinguished the endemic subspecies *britannicum* confined to this country and evidently an oceanic type, the markedly continental subspecies *decussatus* of Poland and Russia, and the subspecies *vulgare* occupying an extensive intermediate range, such segregation is clearly a necessary preliminary to any ecological assessment of the relation to habitat conditions of these plants.

Wilmott has pointed out that the British lungwort, *Pulmonaria angustifolia*, is the Atlantic *P. longifolia* (Bast.) Kern. and not the Continental *P. azurea* Bess. (in *Peuplement des Îles Britanniques*, Paris, 1930). Stapf showed that our English aconite, *Aconitum anglicum* Stapf., is an endemic species and not therefore to be expected to show the same ecological requirements as the Continental *A. napellus* with which it had so long been confused (cf. Stapf, *Bot. Mag.* t. 9085, 1926). To the systematist too we owe the recognition that the arum of the Isle of Wight is not the Mediterranean *Arum italicum* Miller, but a species of southern England and northern France which Townsend distinguished as a variety and Ridley has recently raised to specific rank under the name *Arum neglectum* (*J. Bot.* p. 144, 1938).

If it had not been for the studies of Schulz we might have long continued in the belief that the *Phyteuma* of our chalk downs was the continental *P. orbiculare* whereas it is in reality a variety of the oceanic species *P. tenerum*. Again Newton showed that our *Silene otites* is not the plant of central Europe but a type most closely allied to those found in Denmark.

Until such segregates are distinguished the marked soil preferences or climatic tolerances of species are liable to be overlooked. So, too, the recognition of the critical segregates in such genera as *Viola*, *Salicornia*, *Statice*, to mention but three examples, has revealed a relation between phenotype and habitat that was entirely obscured until the Linneon aggregate underwent subdivision at the hands of the systematist.

It is hardly necessary to stress the waste of labour and confusion that may result from failure to apprehend lack of homogeneity in the material which the ecologist studies.

The debt that British ecologists owe to such systematists as Dr Turrill and Mr Wilmott, who are constantly studying and comparing the British and Continental material, to the many systematists who have given critical study to particular genera, is so obvious that it would be superfluous to stress that debt were it not that in approaching the second part of my task, namely the criticism of the taxonomist by the ecologist, I do so only in the spirit of that gratitude which has been defined as a lively sense of favours to come.

I have already laid emphasis upon the ecologist's need for the finer subdivisions, but this does not mean that the ecologist always welcomes the extreme subdivision of species in which monographers sometimes indulge. When based mainly or entirely on herbarium material such monographs are liable to be both a snare and a delusion.

The ecologist requires to identify the living plant in the field and should, and often does, acquire a knowledge of "spot characters" by which a species can be identified with certainty even when in the vegetative condition. But too often the characters in monographs are so obviously designed for identification in the *Hortus siccus* that the utility to the ecologist is much impaired. Is it too much to ask that their needs should also be catered for?

One welcomes the increasing tendency for monographers to cultivate the plants they name since the designation of ecads as hereditary types is liable to cause as much confusion as failure to segregate types that are in fact genotypically distinct.

The points of view of the ecologist and taxonomist are admittedly different. The taxonomist naturally seeks for distinct and constant, preferably absolute, distinctions of a morphological character. The more constant and less relative the more suited to his purpose. Hence the characters of those organs, which are most important physiologically, which play the greatest part in determining success in particular environmental conditions, and which are most important for failure or success in competition with other organisms, are just those least suited to the taxonomist's purpose.

The taxonomist searches for characters that are not only constant through the diversity of habitat conditions but also those that have remained relatively stable through the many vicissitudes of phylogenetic change. Is it to be wondered at then if his point of view is morphological and static rather than physiological and dynamic. Hence it is we find that not only some taxonomists but even descriptive ecologists reared in the taxonomic tradition indulging in the naïve belief that a distributional discontinuity in the past, which may even be a hypothetical one, is a sufficient explanation for a continued and continuing discontinuity in the present.

The ecologist, if he is a scientific ecologist, should be primarily interested in the physiology of the species either as individuals or as communities and hence attaches the greatest importance to just those features which the taxonomist is apt to ignore.

The ecological importance of a biotype may depend on its potentialities such as, for example, the capacity to grow tall, to develop a high suction pressure, to produce deep roots, but it may be some more subtle feature. The widespread and apparently complete replacement of the scented *Mimulus moschatus* by the scentless type may be instanced as affording a significant example of what may perhaps be a commoner phenomenon than we imagine.

The fact that this replacement has occurred not only in England and elsewhere in Europe, where the plant has been in cultivation, but also in the Eastern States of America, where it was introduced, as well as in the western States where the species is native, renders it almost certain that we are here concerned with the replacement of one genotype by another of greater survival value.

It is scarcely to be supposed that the supremacy of the scentless Musk is a direct concomitant of its scentless character but that this lack of scent is probably merely the symptom, as it were, of those physiological differences that have ensured its success.

But we can scarcely doubt, from the known history of events, that this replacement of one genotype by another would have passed entirely unnoticed had it not been for the comparative conspicuity of the lost character.

The biological importance of the distinctions between the two genotypes is so fundamental as apparently to have led to the extinction of the scented race, yet the morphological distinctions, if they existed, were sufficiently insignificant to have passed unnoticed.

It is quite evident then that we cannot adopt the complacent assumption that internal changes which are of vital ecological significance will always, or even usually, be accompanied by changes of external form of sufficient magnitude to call for separation by the taxonomist, be he never such a splitter. Such types will normally be either ignored by the systematist or regarded as trivial though to the ecologist their importance may well be far greater than that of organisms whose morphological distinctions are conspicuous.

We cannot expect the taxonomist to make physiological species. The idea of physiological type specimens might excite the habitual controversialists but scarcely commends itself to those of us who are concerned with knowing without probability of error what the other worker is writing about. But if physiological species are an unattainable ideal the closest co-operation between the taxonomist and the ecologist is necessary and both aspects must develop side by side unless the one is to be a limiting factor in the development of the other.

It is the different point of view from which the organism is approached and to which I have already alluded, which constitutes the chief basis of criticism applying to both classes of observer. It often leads the ecologist to under-rate the importance of a meticulous taxonomy, it sometimes misleads the taxonomist into believing himself fully equipped for the task of ecological investigation.

3. THE USE OF ECOLOGICAL DATA IN TAXONOMY

By O. W. RICHARDS

THE organizers of the present discussion suffered under two handicaps. First, the words "ecological data" are very vague, because the field covered by ecology has never been adequately defined. Secondly, it may be inferred from the title they chose for my contribution that they were under a profound misconception as to the nature of taxonomy.

Although it does not strictly fall within my terms of reference, I believe that a brief indication of the lines along which a precise definition of the science of ecology might be reached will make clearer the relation between ecology and taxonomy.

In this country, at any rate, it is difficult to define ecology more closely than by saying that it forms the subject matter of papers published in the Ecological Society's Journals. It includes, therefore, anything from the physiology of a single plant species to accounts of travel in remote regions, from the enumeration of the birds' nests in an English county to studies of the fluctuations of protozoal populations in petri dishes. It might be convenient to retain the word *oecology* for this heterogeneous collection of biological research. Oecology is a mixture of three separate sciences: *physiology*, *taxonomy* (including biogeography) and studies of fluctuations in the densities of animal and plant populations, to which I would restrict the term *ecology*. The distinction between these three separate sciences is nearly always easy to draw in studies of animals. In the case of plants, the special character of plant associations may make the distinctions less clear-cut, though they are still recognizable. The differences between plant and animal associations clearly depend on the great importance in the former of competition for space and the relative unimportance of this factor in animals, except for a few groups. But I cannot enlarge upon this topic here. The advantage of my proposed definition is that it marks off for investigation a large subject not dealt with under any other heading; one moreover which requires quite special and peculiar techniques.

The fundamental misconception of the nature of taxonomy conveyed in the title of my contribution lies in the suggestion that taxonomy deals with dead organisms and that the classification of these may be improved by occasional examination of what they do when alive. But a dead specimen can only in a very abstract sense be said to be a member of a species at all. A species can only express itself during a definite period of time—at least long enough to include one complete life-cycle. Moreover, a species has a geographical distribution which is one of its most important characters. The title, therefore, which I would have preferred would have been, "The relative importance of field (or physiological) and morphological data in taxonomy."

There are four ways in which the success of a taxonomic study may be tested. The first is by the use of the work for actual identifications. This is a severe practical test but cannot provide any theoretical justification for the scheme of classification. The second is by genetical experiments which as a rule have only a limited application. The third is by the discovery or co-ordination of palaeontological evidence which, again, is only rarely available. The fourth (exactly analogous to one of the ways in which the Periodic Table of the elements has been justified) consists in showing that new or imperfectly known species possess properties which can, at least to a considerable extent, be predicted from the system. One could, of course, be satisfied merely with the demonstration that the set of morphological characters which define a species or a genus continue to be found in association as the material available for study increases. But the classification will be far more useful to more people and, in my opinion, more likely to be sound even on the restricted morphological plane, if as far as possible *all* characters of a species have been brought into one scheme. This is not only because more characters are made available for study but also because predictions can be made in more than one field. To take an example, there are about two hundred and fifty wasps of the genus *Trypoxylon* found all over the world. Wherever they have been studied, they have been found to build nests of mud which they stock with spiders. "Mud-nests" and "spider-prey" are clearly generic characters of the same importance as the morphological details more often mentioned in taxonomic works. Although this seems a very simple statement, the consistent adoption of this viewpoint makes a very considerable difference to the sort of taxonomic work produced; the knowledge that certain species share peculiar habits may often lead one to look for and discover unexpected morphological similarities.

It is true that structure must be studied before habits and physiology. Moreover, it is as a rule only the structural characters of a species which can be preserved in museums, though far more could be done in the way of labelling specimens more fully with field data. For purely *practical* reasons of convenience, I would restrict the term *species* to forms which can be identified in at least one sex from *dead adult* specimens. Nevertheless, in malariology for instance, it is equally necessary for no less practical reasons (i.e. differences in likelihood of malarial transmission), to recognize *subspecies* of mosquitoes which scarcely differ at all in the morphology of the adults, though they differ in their early stages and in their mating-habits. These subspecies are of the same essential nature as others which are more distinct morphologically, but I believe it would lead to more confusion than the logical uniformity would compensate for if binomial Latin names were given to forms which museum workers could not usually hope to identify.

To consider, now, the value to taxonomists of the sort of data provided by ecologists in the broad sense. In the first place, data which are not quantitative are only of limited use to anybody, and this of course applies equally to mor-

phological studies, except in the earliest stages of constructing a classification. It is essential that the abundance of species should be expressed numerically and that there should be a definite indication as to their spatial distribution (i.e. whether aggregated into colonies or evenly spread); in the case of plants, information as to the size of individuals and average numbers of leaves and flowers are essential if the work is to be basic to animal-studies. Again, it is only of little use to measure the physical factors of each habitat if the correlations between abundance of organisms and the intensity of each factor are not determined. I believe that the correlation coefficient is one of the most powerful tools available for the study of advanced taxonomy, of ecology (in my sense) and of evolutionary problems. It can only be used when all relevant factors have been evaluated numerically, but it may well prove to be the only way in which various field problems which appear almost insoluble can be investigated.

Finally, I wish to repeat that I regard most of what is called ecology as either specialized taxonomy or as comparative physiology. The line between taxonomy and physiology is not easy to draw, but the most important criterion is that taxonomists are interested in the differences between species, while physiologists are mainly concerned with the resemblances between them. Whether a study is made of differences in the reactions of species or of their morphology, the work is still essentially taxonomy. As for ecology in the restricted sense, its relation to taxonomy is mainly in one direction. Ecology may have some value in supplying museums with abundant material. But much ecological work, at any rate in insects, is held up because essential taxonomic revisions are still incomplete.

4. ECOLOGY AND TAXONOMIC DIFFERENTIATION

By J. S. HUXLEY

TAXONOMY has two aims: the practical and immediate aim of naming and pigeon-holing natural diversity, and the intellectual and ideal one of giving a scientific description of it.

In what follows I shall assume the modern selectionist view, as developed deductively by Fisher, Wright, Haldane, and Timofeeff-Ressovsky, on the basis of the facts of neo-Mendelism.

I shall not deal with higher systematic categories, except to say that, in point of fact, a far greater number of those than is often supposed have some ecological basis, in regard to way of life (cf. the orders of Mammalia). This is often disguised through morphologists taking some correlated morphological character as diagnostic.

I shall confine myself to what Rensch (1934) has called natural, objective,

or biologically real systematic units, self-reproductive *qua* groups, reproductively isolated in whole or in part, and with some degree of morphological or other difference from other similar groups, and with a distinctive area of distribution.

Those include subspecies in the strict sense, and species, both mono- and polytypic. The category further comprises the small local groups which may be distinguished as *micro-subspecies*. There are also the groups which we may call supra-species, including a number of forms, some of which may have differentiated into good species, but of which we can be certain that they have arisen from a common ancestral group *via* geographical isolation: although such groups no longer possess reproductive unity, they have not long lost it, and may also be considered. As a zoologist, I shall confine myself almost entirely to animals.

Such natural systematic units arise only as a sequel to some form of isolation, partial or complete, be it genetic, geographical, ecological in the narrow sense, physiological, or reproductive. The last three categories may be conveniently lumped together as ecological in the broad sense: then we have three main types of isolation, due respectively to separation in space, to differentiation of function or way of life, and to accidents of the genetic mechanism.

Geographical separation is usually combined with some degree of ecological difference. However, even when it is not, it may lead to taxonomic differentiation if the isolation is complete and the population small. Then, as Sewall Wright (1939) has shown, accidental events may override selection, non-adaptive recombinations become typical of the group, and selectively neutral or even deleterious mutations become incorporated in its germ-plasm. This is why local populations of sedentary fish show marked non-adaptive as well as adaptive differences (Schmidt, 1918) and why mere distance may promote more differentiation in them than do differences of habitat (Thompson, 1931). The "micro-subspecies" of various grasshoppers may similarly show extraordinary diversification, each little isolated colony sometimes differing from every other (Uvarov, *in verbis*). This also explains why the populations of groups of small islands or of lakes are often markedly different, the degree of differentiation being often far greater than on a much larger total area of mainland or of a single large body of water (for mammals, see Miller, 1909; for lizards, Kramer & Mertens, 1938; for fish, Worthington, 1939). Kramer & Mertens have established a marked negative correlation between the degree of divergence of lizard populations and the size of the islands they inhabit—a beautiful confirmation of Wright's deductive conclusions.

Accidental differentiation of isolated populations may also occur owing to "sampling errors", the colonizers of a new isolated area not being a representative sample of the population from which they are drawn (Partula: Crampton, 1936, 1932).

In these cases we have taxonomic differentiation wholly or chiefly in the absence of ecological difference, or overriding it—in any case not correlated with it. More to our present point are cases where the two are correlated. We may distinguish three main grades of ecological difference, concerned with climate, with habitat, and with physiology respectively.

With specific and subspecific differentiation, climatic influences usually come into play in addition to purely geographical isolation. The resultant differences in the taxonomic groups, when not accidental (see above), may be either directly or indirectly adaptive. Direct adaptation is seen, e.g. in protective resemblance to background colour (see Sumner, 1929; Dice & Blossom, 1937; and discussion in Huxley, 1939). Indirect adaptation may be safely assumed in the numerous cases where the group characters are graded in correlation with some environmental gradient, and especially when a similar correlation is repeated in parallel in many related forms (see Rensch, 1936, 1938; Vogt, 1909, 1911; Mayr & Serventy, 1938; discussions in Rensch, 1929, 1936 and Huxley, 1939). In some cases apparently adaptive internal characters have been discovered (e.g. thyroid structure in deer-mice; Yocum & Huestis, 1928), the visible characters of colour and body-proportions being “correlated characters” in Darwin’s sense.

Climate may also have further effects on taxonomy by inducing changes of range. These have been of major extent during and since the last glacial (pluvial) epoch. Taxonomically, the most important type of change has been the separation of a population into two, followed by climatically-adapted differentiation and often by post-glacial re-meeting of the two groups.

When differentiation has gone far enough, the result is that two good species are found where otherwise only one would have existed; as in central European tree-creepers (*Certhia familiaris* and *C. brachydactyla*; see Rensch, 1934, 1937). Interestingly enough, one of the two species here involved, the northern tree-creeper (*C. familiaris*) is involved in a somewhat similar situation in the Caucasus (Dementiev, 1938): here, however, the differentiation between the two forms, presumably separated by the Ice Age, has not gone beyond that of subspecies (*C. f. familiaris* in the north and *C. f. persica* in the south, with the result that the region where they later re-met (the Caucasus) is filled with a very variable hybrid population.

Where differentiation has been slight, interbreeding gives merely a population of unusually high variability, as in central European bullfinches (*Pyrrhula*), longtailed tits (*Acredula*), etc. Meeting after an intermediate degree of differentiation gives more spectacular types of variation in the interbreeding zone—either a large irregular area is entirely populated by hybrids (moths, *Platysamia*: Sweadner, 1937), or there is a broad belt (*Colaptes*: see Bateson, 1913) or a narrow one (*Corvus*: Meise, 1928) showing hybridity and Mendelian segregation. The breadth of the hybridizing area is presumably inversely correlated with the degree to which the differentiation of the pure

types has proceeded, either with regard to reduced fertility on crossing or with regard to the harmonious stabilization of their distinctive gene-complexes (see discussion in Huxley, 1939). The greater the selective disadvantage of the hybrids, the narrower the hybrid zone will be.

Ecological differentiation in regard to habitat is well shown in certain deer-mice (*Peromyscus*: see Dice, 1931). Here two subspecies, though inter-fertile in the laboratory, retain their distinctness in nature though found in the same geographical region. This is accomplished through their being confined to different habitats: one is restricted to forests, the other to open country. Similar cases in insects are cited by Pictet (1928) and in birds by Dementiev (1938), the two types being often confined to different altitudinal zones.

It used to be assumed that most cases of climatic (geographical) and ecological adaptation to environment were modifications due to the direct action of external conditions. It has now been shown, however, that the great majority of such cases in higher animals and quite a large number in plants have a genetic basis (Rensch, 1934, 1936; Dobzhansky, 1937). It is in any case impossible to decide without experiment, though this is much more necessary in plants (see Turrill, 1939), where some species prove to be highly plastic, others highly resistant to environmental change, and genetically some are very variable and others possess but a small variance.

Wherever marked modificability exists, Baldwin's and Lloyd-Morgan's principle of Organic Selection may operate, in which Lamarckism is simulated by the group being temporarily adjusted to new conditions by modifications, but later genetically adapted by the capture of such favourable mutations or recombinations as may arise.

It is probable that many more cases of purely ecological isolation will be discovered in regard to subspecies as well as to species. For them we shall then need a "principle of ecological replacement", analogous to that of geographical replacement on which geographical subspecies (and species of a supra-species) are diagnosed (Rensch, 1929, 1934).

A special case of such ecological replacement, with consequent biological isolation and the formation of partially or wholly discontinuous group-units, is seen in the numerous "physiological races" of parasites and phytophagous insects (summaries by Thorpe, 1930, 1939).

The important fact for taxonomy emerges, that although the groups thus formed may show as complete reproductive isolation as the most obvious of "good species", their morphological distinctions may be slight or apparently absent, so that museum workers not unnaturally hesitate to assign specific names to them. The solution will perhaps be to assign them specific names, but also to retain a broad binomial for the whole set. This latter name should of course be different from any of the separate specific names, and might be distinguished by the abbreviation (*sp.l.*) (= *species lata*).

Precisely the same practical problem presents itself in the case of the

"races" of malaria mosquitoes (*Anopheles*) and other related Diptera recently discovered and investigated by Hackett, Missiroli, Swellengrebel and others (see discussion in Thorpe, 1939). Here, however, the mode of their isolation is unknown, and they appear to constitute a new *type* of taxonomic unit. They show definite ecological preferences and also some difference in geographical distribution: but neither geography nor ecology keeps them from overlapping, and sterility barriers are known for some at least.

Another eco-taxonomic puzzle is provided by the limpets (*Patella*: Fischer-Piette, 1935). In some regions, three distinct species are to be found, and have their own ecological preferences in the tidal zone: but in other regions the three types are merged into a single interbreeding population covering all of the tidal zone.

Genetical isolation depends on occurrences in the chromosomal mechanism, of such a nature that they constitute barriers, of some degree of efficiency, to full fertility. They may produce complete isolation at a bound, as between triploids and diploids, or in allotetraploids formed after hybridization. More frequently they produce only partial isolation, which must later be rendered complete by means of single-gene mutations. This appears to be the usual course of events after inversions or translocations (cf. *Drosophila simulans* and *D. melanogaster*, etc.; discussion in Dobzhansky, 1937, and Muller, 1939).

An interesting feature of this last type of case from our present point of view is that, since the two types are inhabiting the same region and do not differ in their original complement of genes but only in their arrangement, there will be little or no reason, either adaptive or constitutive, for them to differ morphologically. In point of fact they are often extremely alike (*Drosophila simulans* and the division of *D. pseudoobscura* into intersterile "races" had completely eluded the museum taxonomists), and it is only gradually that the accidental accumulation of gene-differences comes to cause any visible differentiation. This again poses questions for the taxonomist. Should intersterile groups, like races *A* and *B* of *D. pseudoobscura*, be styled species, though morphologically and ecologically so similar?

In the case of autopolyploids conditions are rather different. Here the alteration of the ploidy itself brings about certain ecologically important changes. Normally, anisoploids can only survive if apomictic: this applies to animals as well as plants (see Vandel, 1937). In general, increase in chromosome number is correlated with slower growth and more perennial habit (see summary by Müntzing, 1936). Further, certain experimental autopolyploids show in general a higher water-content, a longer vegetative period and a lower rate of cell-division. All these changes alter the ecological predisposition of the type, as is shown by the further fact that polyploid types tend to occur in more extreme habitats than the related diploids (see Babcock & Stebbins, 1938).

If we contrast all the types of isolation as regards the degree of morphological and other differentiation they tend to promote, we shall find something

of the following sort. Geographical isolation tends to produce, in addition to accidental divergences due to the Sewall Wright effect, slight differences of colour and proportion, directly or indirectly correlated with broad climatic differences; it will not, however, tend to produce barriers to intercrossing so rapidly as does ecological isolation to different habitats within the same geographical area (cf. the sex-recognition characters, visual or auditory, which keep overlapping bird species apart, e.g. whinchat and stonechat (*Saxicola rubetra* and *S. torquata*), willow-warbler and chiffchaff (*Phylloscopus trochilus* and *P. collybita*): see Huxley, 1938*a*). Ecological isolation, when in relation to habitat, tends to produce definite morphological adaptations, but when in relation to host or food-plant is often unaccompanied by any but the most trivial changes, although inter-sterility dependent on mating preferences tends to be promoted. Finally, genetic isolation originating in intra-chromosomal accidents tends to produce little or no differentiation, whereas that originating in a change of ploidy produces a change in ecological predisposition *ab initio*.

Synecological conditions will also have an effect on differentiation. Worthington, Buxton and others (discussion in Worthington, 1939) have shown that reduction in predator-pressure or other competition will allow much more extensive and more varied adaptive radiation (cichlids and other fish in African lakes; insects on oceanic islands).

The qualitative extreme of this effect is probably to be seen in such cases as the Geospizidae (ground-finches) of the Galapagos, with their great range of diversity in a limited area, and apparently unaccompanied by sharp speciation (Swarth, 1934), and the quantitative extreme in the adaptive radiation of the marsupials in Australia, free from placental competition.

We now come to a less well-explored problem, namely the geographically-correlated variation within areal groups. The best-known aspect of this concerns the so-called geographical rules of Bergmann, Allen, Gloger, etc., recently summarized and extended by Rensch (1936, 1938). According to those, certain characters of related subspecies within their species (or in some cases species within a species-group) change progressively in accordance with some climatic gradient: the characters include absolute size, proportionate size of parts, coloration, etc. Very frequently numerous subspecies of a group show parallel changes within their subspecies (cf. Vogt, 1909, 1911, in bumblebees; and see below).

Salomonsen (1933) and Huxley (1939) have made some quantitative studies of these phenomena: it appears that in passerine birds, the increase of linear dimensions with 1° N. latitude lies between 0.5 and 2.00%.

In spite of the criticisms of Reinig (1937) it seems clear that the *prima facie* interpretation of these regularities as adaptive holds good for the majority of cases (see Rensch, 1938).

An interesting point in certain cases (e.g. Dobzhansky (1933) in coccinellid beetles; Mayr & Serventy (1938) in birds) is that, while the gradations are very

similar, they do not exactly coincide for different species. Thus in Mayr & Serventy's case, numerous species of the Australian bird genus *Acanthiza* show a gradation from dark coastal subspecies to pale forms in the desert interior; but the boundaries of the different colour types may occur at very different distances from the coast in different species. The authors ascribe this to different degrees of evolutionary plasticity during postglacial changes of climate. It is, however, at least equally possible that it depends on differences of reactivity, different species showing different degrees of coloration-change correlated with a given adaptive physiological adaptation to drier climate, or possibly different degrees of the internal physiological adaptation itself. Similarly Dobzhansky's lady-beetles have their palest Old World forms in the dry areas of central Asia; but whereas in some cases the maximum pallor is found in Russian Turkestan, in others it is in Chinese Turkestan, and in still others in Persia. Extremely interesting ecological problems are posed by such taxonomic facts.

The regularities so far mentioned are concerned only with the mean values of characters for various groups. In addition, we may find gradual changes from place to place within the single group. These may concern invisible but strongly adaptive characters (temperature-preference and phototropism in *Carabus*, Krumbiegel (1932); reproductive adaptation to temperature in *Drosophila*, Dobzhansky (1937, p. 157), and in *Lymantria*, Goldschmidt (1934)). Or they may concern visible characters which are usually, it appears, non-adaptive in themselves though correlated with adaptive invisible characters (coat-colour in *Peromyscus*, buffaloes, etc.; examples in Huxley, 1939). A peculiar type of gradient is that in the proportions of two sharply-contrasted types in a dimorphic species. This may be stabilized in relation to the change in selective value of the two characters in ecologically different parts of the range of the species (melanic and "normal" hamsters (*Cricetus*); see Timofeeff-Ressovsky, 1939; and for other examples where we may presume a similar balance, see Ford, 1939). In some such cases of "dimorph-ratio gradients" (tooth-characters of *Microtus arvalis*; Zimmermann, 1935) the gradient seems to have come into being merely as the result of the occurrence of a mutation with positive selective value and its subsequent more or less concentric spread, and not to be correlated with any environmental gradient.

For such character-gradients in general Huxley (1938*b*, 1939) has proposed the term *clines*. To distinguish the inter-group and intra-group clines, perhaps *exoclines* and *endoclines* will serve.

Clines may be correlated with broad geo-climatic gradients or with gradients in ecological habitat (*geoclines* and *ecoclines* respectively). In addition *genoclines* may exist, i.e. with a purely genetic basis, depending on the rate of gene-flow across an interbreeding zone. I have already given some examples of geoclines. Among animals ecoclines may occur in land-snails (Rensch,

1934, pp. 3, 79); in plants they are probably more common. In *Plantago maritima* Gregor (1938) has shown that they are brought into being by selection, each type of habitat having a small section of the total large array of genetic types, which is adapted to it.

Exoclines and endoclines may be combined in a general cline of the type of a stepped ramp, the slope of the endoclines being always less than that of the exoclines (e.g. *Peromyscus*, *Parus*: see Huxley, 1939).

One of the most interesting relations between taxonomy and ecology concerns the formation of readily distinguishable subspecies within a biologically continuous population. Such subspecies usually cover considerable areas, and are separated from each other by narrow intergrading zones, where interbreeding produces intermediates (*Troglodytes*, *Lanius*, *Peromyscus*, etc.: see Huxley, 1939).

The problem poses itself as to why in such cases the subspecies are so relatively constant over such large areas and how the intergrading zones are kept so narrow, in spite of gene-flow between the two types. If, as will usually be the case, the two subspecies differ adaptively, one might *a priori* expect a much more gradual character-gradient, even a single uniform geocline, in place of the staircase effect actually found, with the cline restricted to a short sharp genocline between the two types. Why is there more abrupt change and more discontinuity in the systematic units than in the environmental conditions?

In reply to this question we may first suggest that in addition to the sharp genoclines constituting the intergrading zones, further gradual geoclines will often be found extending throughout the subspecific areas or at any rate across a broad marginal zone (e.g. *Peromyscus*, *Parus*, etc.: see Huxley, 1939). More importantly, the principle of harmoniously stabilized gene-complexes (Timofeeff-Ressovsky, 1932, 1939; Fisher, 1931; discussion in Huxley, 1939) will see to it that wherever the ecological difference between the centres of the subspecific areas is sufficient, a "biological tension" will result, which will produce *partial discontinuity* between the two groups. Each group will evolve a gene-complex which is not only broadly adapted to the external environment of the central area of its range, but is also harmoniously stabilized, in adaptation to the internal genetic environment, by the selection of modifiers. Crosses between the two types will lack this stabilization, and will therefore be at a selective disadvantage. The intergrading zone will therefore remain narrow: the intermediates are constantly being brought into existence by intercrossing, but as constantly being extinguished by selection. Further delicacy of adaptation will probably occur through the development of gentle clines within each subspecific area, as already suggested.

The intergrading zones of partial isolation will naturally tend to occur in correlation with rapid change in environmental gradients, or where there is low population density. But they may come into existence without any such

correlation and may be maintained even in spite of range-changes of the subspecies concerned (see Huxley, 1939).

It is worth while remembering that such range-changes may be of large extent and may be proceeding rapidly at the present day: the serin finch (*Serinus canarius*) has spread from south to north France in the last hundred years (other examples in Timofeeff-Ressovsky, 1939) and the Fulmar petrel is extending rapidly southwards round Britain (see S. Gordon, 1936, *Nature*, **137**, 173).

The principle at work is thus somewhat similar to that of the maintenance of comparatively sharp ecological zones in organisms, in spite of gradual change of environment, e.g. the rapid transition from conifer forest to open meadow with altitude in mountainous regions: see Elton's *Animal Ecology*, etc., for a discussion of this point.

It is presumably because of the existence of well-stabilized gene-complexes that many species are able to thrive under very varied conditions: the environmental conditions at the margin of the range in particular are often strikingly different from those near its centre (cf. Bodenheimer, 1938).

The tendency for eco-geographical differences within a continuous continental area to introduce partial discontinuities into a single specific population is of great evolutionary importance since, as Sewall Wright has shown (see Wright, 1939), species thus partially isolated into subspecies possess the highest degree of evolutionary plasticity and potentiality. It will be of great interest to study the precise degree of ecological difference needed to produce partial and total biological discontinuities respectively, in relation to different modes of life.

Another problem of great general interest concerns the fact that geographical subspeciation appears to be much commoner in animals than in plants, while ecoclines on the other hand seem to be less frequent in animals. These and numerous other points of difference in the minor taxonomic differentiation of the two kingdoms demand intensive analysis and comparative treatment.

It remains to consider certain practical aspects of the study of the ecologically correlated character-gradients included under the term clines. How, for instance, shall the concept be incorporated into taxonomic practice, as it must be if taxonomy is to live up to its function as a pure science, descriptive of all the facts of the distribution of organic diversity in nature?

In the first place, specification by exoclines may often be used as an additional method, *subsidiary* to the current practice of conferring subspecific names on areal groups. When a number of groups fall upon a cline, additional meaning is given to the group's relation of connexion, and a synthetic approach is made possible on the ecological plane, analogous to that which has occurred on the geographical plane by uniting groups which replace each other geographically, as subspecies of a polytypic species. The ecological value of this method will be enhanced if further research shows that, in addition to the

general exoclines, the separate groups show endoclines in the same characters, though of course not so steep.

The cline problem forms an important part of what Timofeeff-Ressovsky (1939) calls phenogeography and genogeography (and see Buzzati-Traverso, *et al.* 1938). A further extension of this subsidiary use of clines will occur wherever exoclines for different characters are found to run in different directions (*Lanius* and other birds; see discussion in Huxley, 1939; tooth characters and coat-colour in *Microtus*, Zimmermann, 1935). Specification by clines will then bring out the ecological basis of differentiation with a new clarity.

Similarly, the detection and mapping of endoclines, and the contrasting of cases when they are present with those where they are absent, will throw light on the selective influences operating within populations. The two studies will grade into each other wherever gentle endoclines alternate with steep genoclines, resulting in partial discontinuity of subspecific groups.

Secondly, cases appear to exist where the cline concept may justifiably replace the method of areal naming of groups, either temporarily or permanently.

When there exists a continuous cline of more or less uniform slope, or at least not marked off into relatively stable areas by zones of rapid character change, it appears both illogical and misleading to employ subspecific names to denote mere stages in a continuous progression.

To take an example, Løppenthin (1932), describing the European nuthatches (*Sitta europaea*), states, that for over 1000 km. there exists a continuous gradation from north-east to west and south between those with white underside and those in which the underside is quite deep rufous, and further that it is impossible to draw any sharp lines between distinguishable groups. Nevertheless, he classifies the species in this area into five named subspecies, adding two further "types" of intermediate nature. It would appear much more satisfactory in such cases to retain subspecific names only for the two end-terms of the series, partly on grounds of convenience, and partly because such terminal forms do (as in this instance) appear to be relatively constant over considerable areas, and to refer to the remainder merely as numbered stages in a specified cline. In this case we would specify *Sitta e. europaea*, *S. e. caesia*, and cline *S. e. europaea-caesia*. By such means we obviate giving the false impression that stages in a continuous gradient are biologically comparable with true subspecies, which must be more or less sharply delimited, either by full geographical isolation, or by the partial discontinuity provided by narrow intergrading zones of rapid change. It seems probable that the African buffaloes and squirrels, described by Christy (1929) and Ingoldby (1927) respectively, will best be described in similar terms, as also the gradations across broad areas of apparent hybridization such as that described by Sweadner (1937) for the moth *Platysamia* in North America.

If this is accepted, it follows that cases in which it is doubtful whether

delimited subspecies or continuous clines exist will provisionally be best described in terms of clines. This will often occur when collections have only been made at localities separated by considerable intervals. For instance, Thomas & Wroughton (1916) describe seven subspecies of a species of *Callosciurus* from a limited number of collecting stations along 250 miles of the east bank of the Chindwin river; but they also mention that two localities yielded specimens intermediate between two of their "subspecies". Their data indicate that the facts can be equally well represented by assuming two clines, separated by a tributary. In such cases the provisional use of the cline concept will obviate the cumbering of the nomenclature with subspecific names which may later have to be withdrawn.

In conclusion, it may be said that the general recognition that the differentiation of most of the categories of minor systematics has a direct or indirect selective basis, with a modicum of random non-adaptive change superadded as a result of the isolation of small populations (see Fisher, 1930; Haldane, 1932; Dobzhansky, 1937; Muller, 1939; Timofeeff-Ressovsky, 1939; S. Wright, 1939), implies a much closer tie-up between taxonomy and ecology than has been considered probable in the past (see Robson & Richards, 1936). Ecological conditions will give the clue to many taxonomic facts, and special terminology, through terms such as *ecotype* and *cline*, must be devised (see Turrill, 1939) to bring out this interrelation of the two branches of biology more clearly and to illuminate taxonomy with ecological significance.

For this to occur, however, it will be necessary to combine ecological (and genetical) work with taxonomy to a much greater extent than in the past. Apart from *ad hoc* investigations, this will be realized by establishing experimental departments attached to the world's great museums and herbaria.

REFERENCES

- Babcock, E. B. & Stebbins, C. L. "The American species of *Crepis*." *Publ. Carneg. Instn.*, no. 504, 1938.
- Bateson, W. *Problem of Genetics*. Oxford, 1913.
- Bodenheimer, Z. S. *Problems of Animal Ecology*. Oxford, 1938.
- Buzzati-Traverso, A., Jucci, C. & Timofeeff-Ressovsky, N. W. "Genetica di popolazioni." *Ric. Sci.* (2), year 9, 1, 3, 1938.
- Christy, C. "The African buffaloes." *Proc. Zool. Soc., Lond.*, p. 445, 1929.
- Crampton, H. E. "Studies on the variation, distribution, and evolution of the genus *Partula*, etc." *Publ. Carneg. Instn.*, nos. 228, 410, 1916, 1932.
- Dementiev, G. P. "Sur la distribution géographique de certaines oiseaux paléarctiques, etc." *Proc. 8th Int. Congr. Ornith.* (Oxford), p. 243, 1938.
- Dice, L. R. "The occurrence of two subspecies of the same species in the same area." *J. Mammal.* 12, 210, 1931.
- Dice, L. R. & Blossom, P. M. "Studies of mammalian ecology, etc." *Publ. Carneg. Instn.*, no. 485, 1937.
- Dobzhansky, T. "Geographical variation in lady-beetles." *Amer. Nat.* 67, 97, 1933.
- Dobzhansky, T. *Genetics and the Origin of Species*. New York, 1937.
- Fischer-Piette, E. "Systématique et Biogéographie: les Patelles d'Europe et d'Afrique du Nord." *J. Conchyliol.* 79, 5, 1935.
- Fisher, R. A. *The Genetical Theory of Natural Selection*. Oxford, 1930.
- Fisher, R. A. "The evolution of dominance." *Biol. Rev.* 6, 345, 1931.

- Ford, E. B.** "Polymorphism and taxonomy." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Goldschmidt, R.** "*Lymantria*." *Bibliogr. genet.* **11**, 1, 1934.
- Gregor, J. W.** "Experimental taxonomy II." *New Phytol.* **37**, 15, 1938.
- Haldane, J. B. S.** *The Causes of Evolution*. London, 1932.
- Huxley, J. S.** "The present standing of the theory of sexual selection." In *Evolution*, ed. G. R. de Beer, Oxford, 1938a.
- Huxley, J. S.** "Clines: an auxiliary taxonomic principle." *Nature, Lond.*, **142**, 219, 1938b.
- Huxley, J. S.** "Clines: an auxiliary method in taxonomy." *Bijdr. Dierk.* **27** (in the Press), 1939.
- Ingoldby, C. M.** "Notes on the African squirrels of the genus *Heliosciurus*." *Proc. Zool. Soc., Lond.*, p. 471, 1927.
- Kramer, G. & Mertens, R.** "Rassenbildung bei west-istrianischen Inseleidechsen, etc." *Arch. Naturgesch. (N.F.)* **7**, 189, 1938.
- Krumbiegel, I.** "Untersuchungen über physiologische Rassenbildung." *Zool. Jb. (Syst.)* **63**, 183, 1932.
- Løppenthin, C. M.** "Die Farbenvariation der europäischen Baumkletter." *Vidensk. Medd. Dansk naturh. For.* **94**, 147, 1932.
- Mayr, E. & Serventy, D. L.** "A review of the genus *Acanthiza* Vigors & Horsfield." *Emu*, **38**, 245, 1938.
- Meise, W.** "Die Verbreitung der Aaskrähe (Formenkreis *Corvus corone* L.)." *J. Ornith.* **76**, 1, 1928.
- Miller, G. S.** "The mouse-deer of the Rhio-Linga archipelago, etc." *Proc. U.S. Nat. Mus.* **37**, 1, 1909.
- Muller, H. J.** "Bearings of the *Drosophila* work on systematics." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Müntzing, A.** "The evolutionary significance of autopolyploidy." *Hereditas, Lund*, **21**, 263, 1936.
- Pictet, A.** "Le déterminisme des proportions numériques, etc." *Rev. Suisse Zool.* **35**, 241 and 473, 1928.
- Reinig, W. F.** *Elimination und Selektion*. Jena, 1937.
- Rensch, B.** *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung*. Berlin, 1929.
- Rensch, B.** *Kurze Anweisung für zoologisch-systematische Studien*. Leipzig, 1934.
- Rensch, B.** "Studien über klimatische Parallelität der Merkmalsausprägung bei Vögeln und Säugern." *Arch. Naturgesch. (N.F.)*, **5**, 317, 1936.
- Rensch, B.** "Bestehen die Regeln klimatischer Parallelität bei der Merkmalsausprägung von homöothermen Tieren zu Recht?" *Arch. Naturgesch. (N.F.)*, **7**, 364, 1938.
- Robson, G. C. & Richards, O. W.** *The Variation of Animals in Nature*. London, 1936.
- Salomonsen, F.** "Troglodytesstudien." *J. Ornith.* **81**, 100, 1933.
- Schmidt, J.** "Racial studies in fishes. I." *J. Genet.* **7**, 105, 1918.
- Sumner, F. B.** "The analysis of a concrete case of intergradation between two subspecies. I and II." *Proc. Nat. Acad. Sci.* **15**, 110, 481, 1929.
- Swarth, H. S.** "The bird fauna of the Galapagos islands, etc." *Biol. Rev.* **9**, 213, 1934.
- Sweadner, W. R.** "Hybridization and the phylogeny of the genus *Platysomia*." *Ann. Carneg. Mus.* **25**, 163, 1937.
- Thomas, O. & Wroughton, R. C.** "Scientific results from the Mammal Survey. XII." *J. Bombay Nat. Hist. Soc.* **24**, 224, 1916.
- Thompson, D. H.** "Variation in fishes as a function of distance." *Trans. Ill. State Acad. Sci.* **23**, 276, 1931.
- Thorpe, W. H.** "Biological races in insects and allied groups." *Biol. Rev.* **5**, 177, 1930.
- Thorpe, W. H.** "Ecology and the future of systematics." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Timofeeff-Ressovsky, N. W.** "The genogeographical work with *Epilachna chrysomelina*, etc." *Proc. 6th Int. Congr. Genet.* **2**, 230, 1932.
- Timofeeff-Ressovsky, N. W.** "Mutation and geographical variation." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Turrill, W. B.** "Experimental and synthetic plant taxonomy." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Vandel, A.** "Chromosome number, polyploidy and sex in the animal kingdom." *Proc. Zool. Soc., Lond. (A)*, **107**, 519, 1937.

- Vogt, O.** "Studien über das Artproblem, I und II." *S.B. Ges. Naturf. Fr., Berl.* **28**, 1909 and **31**, 1911.
- Worthington, E. B.** "Geographical differentiation in fresh waters, etc." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Wright, S.** "The statistical consequences of Mendelian heredity in relation to speciation." In *The New Systematics*, ed. J. S. Huxley, Oxford, 1939.
- Yocum, H. B. & Huestis, R. R.** "Histological differences in the thyroid glands from two subspecies of *Peromyscus*." *Anat. Rec.* **39**, 57, 1928.
- Zimmermann, K.** "Zur Rassenanalyse der mitteleuropäischen Feldmäuse." *Arch. Naturgesch.* (N.F.), **4**, 258, 1935.

5. DETAILED TAXONOMY AND AUTECOLOGY

By D. H. VALENTINE

IN investigating the relationship between taxonomy and ecology, there are advantages in using common species, as these may combine taxonomic diversity with a diversity of habitat, and therefore offer a promising field for correlations.

In *Viola Riviniana* Rchb., which is the commonest violet in Britain, two main taxonomic types can be distinguished. The first or "major" type is the common form of woodland and sheltered habitats, and is bigger in all its parts, especially leaves, than the "minor" type, which is a form of exposed habitats such as chalk turf. The "major" and "minor" types retain their characters in cultivation and are probably true-breeding. Taxonomically, the "minor" type corresponds to *forma minor* of Murbeck. Intermediates exist and are under investigation.

Little is yet known of the variability of "minor", but "major" has been shown, by greenhouse work, to be very variable, and breeding experiments indicate that many of the distinguishing characters of the variants are inherited. One of the most interesting is the power of producing adventitious shoots from the roots. So far as is known at present, this is not correlated with any ecological character.

This preliminary classification of *V. Riviniana* is likely to be of immediate use to the ecologist, and may serve as a simple basis for further work. It is highly probable that many British species merit similar investigation. Critical taxonomic revision, coupled with work on autecology and geographical distribution, may throw light not only on the status of the species itself but also on the communities of which it forms a part.

In investigating the geographical distribution of *V. Riviniana*, it has been found that the taxonomy of the European forms is by no means properly worked out, and that their identity with British forms is doubtful; hence we cannot state with certainty the distribution of the British forms. This clearly bears also on comparisons between plant communities in Britain and on the Continent; such comparisons cannot be fully fruitful until ecologists pay more attention to the smaller taxonomic units, and taxonomists to the communities from which they collect.

6. THE MEASUREMENT OF ECOLOGICAL FACTORS OF USE IN TAXONOMY

By C. DIVER

THERE is a tendency in modern biology towards an excessive and unwholesome degree of specialization which must inevitably result in a failure to maintain proper contacts with kindred lines of advance. Neither ecology nor taxonomy can long remain in a healthy state if the workers in these two fields drift too far apart. It will hardly be disputed that experimental and observational biology would become an uncoordinated muddle if it were not for the solid framework which taxonomy has built, and is still building, to support them and to keep them within proper bounds. The ecologist must closely follow the advances of the taxonomist, and must learn to recognize his fine morphological distinctions. For these things mean something. Admittedly in some cases, such as perhaps the clones of apomicts or the hybrid swarms of *Rubus* and *Rosa*, the message is more for the geneticist; but in many cases it is for the ecologist, and unless he can read it the maximum yield will not be obtainable from his work.

On the other hand, the ecologist can contribute to the strengthening and filling in of the taxonomic framework. Habits, range of habitats, and ecological requirements may be as diagnostic of a species as are the details of its morphological structure; and the former attributes need, but seldom receive, as great a precision of measurement and statement as the latter. Both types must ultimately take their place in any description of a species which aims at biological completeness.

In this short contribution I shall deal only with two instances. First, the period of sexual maturity, and secondly, the range of tolerance.

Most systematic works which deal with species having a defined season of sexual activity contain some broad statement which indicates this period. In holometabolous insects this is usually done by stating the months during which the imago is on the wing, or the earliest and latest dates on record. In plants the period of inflorescence is given. But in other groups, where there is no such simple means of demarcating sexual maturity, these statements become more blurred and may even be omitted altogether. One gets the impression that they are often included more as aids to the collector than as statements of biological fact.

If one of the aims of taxonomy is a classification which shows phylogenetic relationships and which allows the maximum number of inferences to be drawn about related species, then the periods of sexual activity must be carefully determined with particular reference to such characteristic differences or shifts as may tend to separate close species between which hybridization and gene-flow might take place. Although we need to know the full possible

period, we must equally know those parts of it during which maximum activity occurs and those in which only stray individuals will be found. In many insects and plants there is a short and sharp period of mass emergence or maximum inflorescence which soon dies away and is delimitable with fair ease from the periods of strays which may precede or follow it. These facts may be expressed diagrammatically as, for instance, Chapman (1934, p. 110) has done in his treatment of the salt marsh plants at Scolt Head Island. His diagrams show that, in those particular circumstances, the period of inflorescence of *Glyceria maritima* is sharply limited to July while that of *Armeria maritima* is evenly spread over the second quarter of the year and then gradually narrows into a long thin tongue of strays stretching to November.

If, in two closely related forms, the periods of maximum sexual activity do not overlap, there is an automatic check upon extensive out-mating, and this barrier should tend in the course of time to accentuate the distinctness of the forms. It may be argued that this is more a genetic than an ecological problem. But fencing off the field into separate compartments does not give the best results. A good instance is that of the five-spot burnet moth, *Zygaena trifolii* Esp. The typical form which frequents moist to dry grassland is usually on the wing from the middle of May to the middle of June. But there is a rather larger subspecies, *palustris*, which is regarded as a marsh form and is on the wing during July and August. Here is an alleged ecological difference associated with, and possibly preserved by, a time shift in the life cycle which takes the marsh form right out of the breeding period of the type, and in fact throws it into that of another close species, the six-spot, *Z. filipendulae* L. This particular case is one which would probably be well worth a detailed ecological enquiry. The work at South Haven Peninsula has shown that there are similar interesting time differences between close species that may live in the same habitat; but these are not fully revealed by the data given in systematic works. This is no criticism of the taxonomist, because it is surely for the ecologist and field naturalist to supply these facts.

If it be agreed that the incorporation of more exact data is the proper aim, then we must consider the process whereby these can be collected and expressed in a concise and practical form. An obvious method is to make, at appropriate intervals, representative sample counts of all sexually mature individuals. In plants this could be expressed as the proportion of the population which was flowering at given times and in given places, since allowance must be made for the shift of the seasons in the passage from south to north. In animals that have an annual life cycle, the frequency of adults in the population would provide a rough measure. Longer lived animals present somewhat greater but not insuperable difficulties. The time-frequency curve for birds can be obtained from counts of nesting pairs.

The South Haven Peninsula records have been collected in a different way and for a different purpose, but they can be used as a rough illustration of this

point (Diver, 1939). Two very close species of the hover-fly genus *Syrphus*, *S. ribesii* L. and *S. vitripennis* Meig., have the same general time range stretching through the seven months from April to October. But for *ribesii* the peak period is May-June with 64% of the records, a period within which only 12% of the *vitripennis* records fall. While, in contrast, 84% of the *vitripennis* records were made in August-September, a period with only 20% of the *ribesii* records. This is a fair example because it is not a simple case, but is complicated by the possibility that there may be more than one brood in a season. Clearly, if such data can be reduced to a statistical form they can be accurately and concisely expressed. It is not necessary here to enlarge on the evolutionary significance of these partial isolations in time.

Exactly the same criticisms apply to the statements usually made about habitats. They are at present given, as they must be, because more exact information is seldom available, in the broadest terms which may completely obscure highly important, though often fine, differences between species. Here, again, what is needed is a numerical statement which will not only reveal the peaks, or optima, but will also show how the frequency of occupation drops off towards the limits of tolerance on either side of the range.

A method for obtaining such data for a small area is now being used with some success at South Haven Peninsula (Diver, 1938). If in any given area all the discrete locus-habitats are listed and classified in terms of their plant-carpet, it will be found that the same type or "species" of habitat will be repeated, in a reasonably varied bit of country, quite a number of times. It is therefore possible to count, for each distinct type of habitat, how many times it is occupied by a particular species; and this figure can be expressed as a percentage of the total number of habitats of that type which are available for occupation. South Haven Peninsula has been classified in this way, and some provisional figures relating to the behaviour of fourteen species of the genus *Crambus* (grass-moths) may be given by way of illustration. Suppose, for simplicity, that there are fifty separate loci which can be broadly classed as "damp heath". Only six out of the fourteen species were in fact found living in this type of habitat. Of these, one was present in, say, 40% of these loci, another in 28%, three in 6%, and one was found once only. Taken the other way, it is possible to class the habitat types, which are occupied by any species of *Crambus*, in eight main groups and to arrange them in a sequence in respect of one attribute, for example, from the driest to the wettest. When this is done it is found that only two species tolerate the whole range of the genus. One has its optima towards the dry end and is less frequently present as the habitats get wetter; while the other is most frequent in the middle of the scale (in "turf" and "*Juncus*-grass") and tails off both to the drier and wetter ends. Another species tolerates five of the habitat types, and the remaining eleven

four or fewer. By this method the main facts about the tolerance of a species could be expressed with reasonable brevity.

The provision of such data falls within the sphere of autecology; but if ranges of tolerance relating to the British Isles as a whole (as opposed to some small area like South Haven Peninsula) are to be included in systematic works, it is necessary for synecology to provide a detailed classification of habitat types with a recognized system of nomenclature. So far as most animals are concerned, habitats are best classified, at least in the first instance, in terms of the plant-carpet; and for the vast majority of species the subdivision of this has to be far finer than some botanists seem prepared to make it for the purposes of plants.

If it be one of the aims of ecology to supply such facts as we have been discussing, then the nexus between ecology and taxonomy becomes very close indeed. For the ecologist can, on the one hand, add vital facts to systematic descriptions and, on the other, provide a testing ground for taxonomic speculations.

REFERENCES

- Chapman, V. J.** "The ecology of Scolt Head Island." *Scolt Head Island*, ed. J. A. Steers, Cambridge, 1934.
- Diver, C.** "The plant-carpet in relation to animal distribution." *Proc. Linn. Soc.* Session 150, pp. 124-35, 1938.
- Diver, C.** "The problem of closely-related species living in the same area." *The New Systematics* ed. J. S. Huxley, Oxford (in the Press), 1939.

7. ECOLOGY AND TAXONOMY: THE TAXONOMIST'S VIEWPOINT

By V. S. SUMMERHAYES AND W. B. TURRILL

THE present contribution to this symposium represents the view of two professional plant taxonomists who are not only deeply interested in ecology but have also carried out a certain amount of ecological research. In being predominantly taxonomic our outlook is therefore rather different from that of some of the previous speakers. At the same time we are able fully to appreciate the advantages to taxonomy of an ecological training and outlook.

Before considering our main thesis, may we take the opportunity of refuting one of the current misconceptions regarding taxonomy still held by some biologists? This is that taxonomy consists largely of delving into musty tomes dating from the eighteenth century or thereabouts and into ideas equally musty and far removed from modern botanical concepts. A certain amount of historical research is usually necessary in any taxonomic investigation but this need not take more than a small proportion of the taxonomist's time. He has therefore ample opportunity of interesting himself in the more dynamic

aspects of modern taxonomy by the consideration of relevant data from such other branches of the science as ecology and genetics.

It is, however, very gratifying to taxonomists to realize that many of their ecological colleagues are desiring closer and closer co-operation with them. From our own experience we are aware that ecologists are tending more and more to send plants to taxonomists for critical determination, are depositing in public herbaria more or less adequate collections from the communities studied by them and are submitting ecological manuscripts for nomenclatural standardization. All this we consider essential for the adequate presentation and recording of the results of ecological research, but unfortunately there are still ecologists who make little attempt to co-operate along these lines. We may quote from a recent number of the *Journal of Ecology* an example which caused considerable hilarity among taxonomists at Kew. A footnote stated that the plant names used in the paper concerned are those of Stapf, *Index Londinensis*. Any taxonomist knows that this work is no more than an index of illustrations arranged alphabetically under the names accompanying the figures cited. Since illustrations of the same species may appear under quite different names, or, on the other hand, figures bearing the same name may represent several different species, it is evident that the *Index Londinensis* neither claims nor possesses any nomenclatural authority. Consultation with workers in any important herbarium or other taxonomic centre would have avoided this curious and misleading error.

May we urge ecologists to co-operate to an even greater extent than in the general ways already mentioned. The data provided with submitted or deposited specimens might well be more complete than is usually the case, since these data may be of considerable value in subsequent phytogeographical or monographic treatment of the material. It is important, however, to emphasize that no complete general schedule of data required by the taxonomist can be prepared, since the information necessary varies from one group of organisms to another. We make the further suggestion that ecologists before starting any investigation, whether synecological or autecological, should discuss with a taxonomic colleague problems which might be of mutual interest.

As regards ecological work in such a country as Great Britain, the flora of which is relatively well known, the taxonomist might well be able to suggest certain small groups of species which could be more extensively collected or about which more detailed data could be accumulated. As examples may be cited the collection of representative samples of populations of spotted and marsh orchids, the recording of the exact distribution of rayed and rayless knapweeds, or that of the varieties of Lesser Celandine with or without axillary cauline tubercles. Often the detailed collection and determination of material of so-called "difficult" genera may provide valuable information for the ecologist, such, for instance, as the exact distribution of paramorphs ("forms") of *Festuca* and *Agrostis* in relation to soil conditions.

In countries of whose flora even our "alpha" or primary taxonomic knowledge is comparatively meagre or at least still far from complete, autecological studies are to a large extent impossible. But for these floras even isolated ecological information may be of great value to taxonomists, such as, for example, the observed restriction of some species to certain types of substratum or to a particular community. For instance, over 60 Balkan Peninsular species or subspecies occur only on serpentine soils, while in British Guiana the Wallaba forest on white sand contains many species which do not occur in any of the surrounding communities. For example, *Catostemma fragrans* (Bombacaceae) is restricted to the Wallaba forests, whereas the allied *C. commune* never grows on the white sand areas. Another type of example is furnished by two closely allied West African species of *Habenaria* which are distinguished, among other characters, by the fact that one (*H. gabonensis*) is apparently always terrestrial, whereas the other (*H. procera*) is apparently always epiphytic; the "apparentlys" are necessary because the essential data have not always been given by collectors.

Another important type of information deals with the duration of the plant, whether annual or perennial, monocarpic or polycarpic. The altitude of the actual specimen collected as well as the approximate altitudinal range, so far as it has been observed by the collector, is also of great importance to both taxonomic and ecological studies. A good example is seen in the distribution of the two species of beech in extreme south-eastern Europe. *Fagus sylvatica* occurs usually on hill slopes at and above 1000 m., whereas *F. orientalis* is limited to the moister, more shady valleys below 800 m.

We also commend to ecologists the practice, adopted by several authors, of publishing as an appendix to an ecological paper isolated observations bearing on the taxonomy of definite species. Such information may not easily be included in the body of the paper and on that account is often omitted; it may, however, be utilized to great advantage by taxonomists working along modern lines.

The taxonomist naturally wishes for ecological data of a kind that he can use as additional diagnostic characters in his classification, especially with regard to the delimitation of species and intraspecific units. With certain conspicuous exceptions there is little direct relation between the habitat (in the broad sense) and the classification of units above the species level. There are, for example, some families almost or quite limited to special habitats, such as Nymphaeaceae and Podostemaceae to an aquatic mode of life and Cactaceae to desert and semi-desert conditions. Sometimes genera or sections of genera are associated with particular external conditions, such as the Batrachian Buttercups. It is at the species level, however, that ecological factors exert the greatest differential influence. This is often due to the very markedly different physiological reactions shown by closely allied congeners. Sometimes these preferences are so very pronounced as to form what is under natural conditions a complete barrier to the amalgamation of the two species into one.

For instance, *Silene Cucubalus* (the common bladder campion) and *S. maritima* (sea campion), which have the same chromosome number and cytologically indistinguishable chromosome sets, can breed together without any trace of genetic sterility and produce fertile offspring. In the wild, however, the populations of the two species keep remarkably distinct and pure, even when in close contact with one another, because of the very efficient natural selection brought about by the habitat preferences already referred to. We may cite another example from the New Zealand flora. *Plagianthus divaricatus* is a divaricating shrub occupying salt-marshes, whereas *P. betulinus* is a tall deciduous canopy tree occurring in lowland forest on good soils. Where the species meet a vast series of hybrids is produced, but on account of the great differences in the habitats occupied by the parents there is only a narrow zone in which the hybrids are found. In this case, however, Cockayne suggests that the hybrids, which are of intermediate life-forms, may be gradually colonizing the forests containing *P. betulinus*.

Apart from using ecological preferences as characters, additional to morphological differences, in distinguishing his species, the taxonomist also requires the collaboration of ecologists in his attempts to classify polymorphic species, whether this polymorphism be due actually to plasticity or to genetical complexity. Indeed only by extensive field observations and experiments can the exact nature of the polymorphism be determined. Turesson's researches have very clearly demonstrated this for a great variety of taxonomic alliances, although his examples have been derived entirely from a north temperate flora. Cockayne and Allan have given similar examples from the New Zealand flora. Taxonomists would welcome the extension of such studies both in temperate and in tropical floras since the herbarium botanist is often faced with the problem of deciding whether certain differences indicate genetic diversity or merely plasticity of one genotype. In the absence of the fundamental data the taxonomist has frequently to reach a conclusion which he knows and frankly acknowledges to be merely tentative.

On the other hand, we should like to emphasize the importance of ecologists not drawing sweeping taxonomic conclusions from short term or insufficiently controlled experiments or observations. For example, the taxonomist finds it very difficult to accept the postulated transmutation by the action of environmental factors of *Phleum pratense* into *P. alpinum* and of *Chamaenerium angustifolium* into *C. latifolium* as recorded in the published results of transplant experiments carried out in America. The British Ecological Society's experiments at Potterne have shown that the genotypes grown retain their specific characteristics in a variety of soils and that the degree of plasticity varies from species to species and cannot be determined by *a priori* considerations. The phenotypic variations shown by the most plastic species tried, namely, *Plantago major*, have indeed been used by certain workers for subspecific and varietal classification of the species, obviously incorrectly.

Even when the phenotypic or genotypic nature of the polymorphism has

been definitely determined, the difficulty of a satisfactory terminology and nomenclature still remains. The taxonomist is sometimes confused by the multiplicity of systems proposed by ecologists to denote the difference between genotypes and phenotypes. There is a considerable amount of overlapping in the use of such terms as ecad, epharmone, ecotype, ecospecies, coenospecies, jordanon, linneon, etc. We suggest that here is a subject of practical importance which might receive the joint attention of taxonomists and ecologists with the object of evolving ultimately a system of terminology and nomenclature which will not only meet the needs of the field worker but which can be related satisfactorily to the International Rules of Nomenclature and to accepted taxonomic practice.

After the status of any given taxonomic unit has been determined with the help of the methods already indicated there is still much to be learnt about it of joint interest to ecologists and taxonomists. For instance, the working out of its life history from the seedling stage, of which we know little in the vast majority of species, up to the dispersal of the mature seeds is of primary importance. To state the matter in even broader terms, we should like to emphasize the necessity of much more autecological work. We fully realize the laborious nature of such studies, but we are convinced that it will not be possible to continue profitably synecological, phytogeographical (including migrational) and even taxonomic studies without knowing much more about the ecology of individual species or small groups of species. Studies whose results have been published, such as those dealing with *Ranunculus parviflorus*, *Eriophorum angustifolium*, *Mercurialis perennis* and *Cladium Mariscus*, have a value far beyond the generally accepted limits of pure ecology, and as taxonomists we should welcome similar studies on many other species. One advantage of such work will be the possibility of providing adequate comparative descriptions of all species, which will not only make handbooks of the various floras of much more general value, but should enable the ecologist to identify his plants at any stage of their development. This is particularly important in statistical work on communities and in the charting of vegetation.

In this paper, we as taxonomists have suggested ways in which the ecologist can provide data of use in systematic studies. It is for the ecologist (as indeed has been done this morning by Prof. Salisbury) to indicate how the taxonomist may help him. For example, do ecologists prefer a narrow or broad view of species? In other words, which do they dislike the more, "lumpers" or "splitters"? This matter is bound intimately to the questions of terminology and nomenclature already touched on.

In conclusion, we should like to state that from our own experience a consideration of ecological and other data not usually regarded as taxonomic adds greatly to the interest of systematic studies in the Herbarium.

8. GENERAL DISCUSSION

Dr J. BURTT DAVY. There is need for some precise definition of such terms as "subspecies", "variety", and "form". Zoologists appear to apply the term "subspecies" to such collections of variants from the type as are called "varieties" by many botanists; it would be helpful to both taxonomists and ecologists if the zoologists and botanists could find common ground for the use of these terms. In dealing with genera of wide distribution it is often possible to draw fairly clear lines of distinction between species occupying opposite ends of the area of distribution; but where the distribution of two or more species overlaps, numerous intergrading variants frequently occur. The question arises whether these variants are hybrids, or whether they represent stages in the development of the "species" occurring at the periphery of the distributional range. Until evidence is available that these variants from the specific types are actually hybrids—if indeed they be such—some term is required by which to designate them; should they be called "subspecies", "varieties" or "forms"?

A second point which it is highly desirable that both botanists and zoologists should consider, is the modern tendency to multiply "genera" by raising to generic rank groups of species which the older taxonomists treated as subgenera. The unfortunate aspect of this multiplication of genera is that it involves a change in the nomenclature of all the species of the subgenera thus raised to the rank of genera. It does not appear that any good purpose is served by such segregation of genera, for the taxonomic differences may be fully emphasized by calling such groups subgenera, which does not involve changes of the name for the species concerned.

Mr A. J. WILMOTT. The fact is that taxonomy is fundamental, since all knowledge is indexed according to the kind of thing to which it relates, and if information is placed under the wrong name it ceases to be fact. No taxonomist can know all groups accurately, and it may be impossible to classify a group until the genetics, cytology, and ecology have been worked out. In critical groups, such as the difficult Arctic *Drabas*, it may take several weeks at the first attempt to train the eyes to discriminate the characters of the kinds and distributions (over the plants) of the peculiar stellate hairs, and even then, after a lapse of a few years, it still takes several hours of study to "get one's eye in" again. The taxonomist tries to be familiar with all the principles and generalizations discovered in genetics, cytology, and ecology which can affect taxonomy, in order to avoid pitfalls and to grasp quickly the various possibilities in the classification of any group. There is no complacency in his mind, but rather is there an acute realization of ignorance. If the ecologist will but have an equally acute realization of *his* ignorance taxonomically one would be content. When the ecologist has this, he will realize that he certainly cannot identify everything accurately, and that material *must* be collected and

deposited somewhere not only for present identification but also for future revision. In many groups *nobody* can identify with accuracy. A competent taxonomist will always tell ecologists which groups it is necessary to collect in this way, and in which a correct identification can be reasonably presumed. There are so many "critical genera" that an ecologist should always work in connexion with a taxonomist. As Prof. Salisbury said, the closest co-operation is necessary. It has been suggested that biotypes should be grown by the taxonomist, but the taxonomist rarely has the time (or opportunity) to do this during his enforced "clerical work", and too often has a long waiting list of those who are hoping for lists from him.

Commenting on matters raised by previous speakers, the request for data on labels may be unreasonable. The important thing is that the extra data should be available, at least in the collector's notebooks, which should be deposited with the collection. As regards the connexion between differentiation and the time lapse (Sewall Wright effect), it may be pointed out that in the Ericaceae there are several species or pairs of varieties or species which are limited to the eastern United States and eastern Asia (Japan and/or China). Sometimes in these widely separated areas the species seem to be identical, sometimes there are two varieties of one species, and sometimes two (rarely more) species. Since this peculiarity of distribution must be presumed to be related to some definite peculiarity of earth history, the time lapse in these cases must be presumed to be identical, and evidently the rate of differentiation must be held to vary. Concerning sterility in *Viola* hybrids, there is an interesting statement by Brainerd that he found hybrids in some of the American violets to be quite sterile in their first year, but producing one or two seeds after two or three years, and in one case becoming completely fertile after seven years. Capt. Diver considers that some might think that matters of hybridization only concerned the geneticist, but it may be suggested that in some groups where hybrids are apparently extremely rare such matters as seasonal climate or unusual conditions might sometimes permit a pollen tube to reach the ovum when in normal conditions it would not do so. Such possibilities should be borne in mind. To give with precision in taxonomic works the periods of sexual maturity would be difficult in view of the great seasonal variation in different years (Glen Clova during a first visit in early June was stated by one who knew the ground well to look like April) and the variation according to latitude (in the Outer Hebrides *Salicornia* flowers in July, not in September). Abundance similarly could not be given from an occasional visit with accuracy; one well-known station for *Trifolium Bocconi* only provided four plants during one visit, but the following year there were large numbers not only there but in all its known habitats at the Lizard (and new stations were discovered that year).

It is desirable to emphasize the need for the elimination from the ordinary nomenclature of species and subspecies—i.e. of the different kinds of *plants*—

of the variations due to simple gene differences, or rather, of their phenotypic differences, which may be termed "phenes". The study of these variations is really a study of the genes (phenes) and their distributions, and not a study of the different kinds of *plants*, and needs a different system of nomenclature special to itself. It might well be that similar differences in allied species are due to the same genes.

Dr B. P. UVAROV. The concept of subspecies is firmly established in zoology, especially in mammalogy, ornithology, and entomology. The subspecies of zoologists is a *geographical* form of a species. There can be at least three different kinds of subspecific variation: (a) continuous, when a widely distributed species varies, e.g. from north to south, and can be divided into several subspecies, not clearly separated; (b) a species spread over several islands (or mountain tops) and represented in each by a somewhat distinct form, which are subspecies separated by small gaps; (c) a species which although widely distributed is always uniform. For the case (a), Prof. Huxley suggested the term "cline", but it appears that the term describes a *phenomenon of variation*, and it is difficult to imagine how it can be used as a term of taxonomy. It appears that the concept of subspecies is less used in botany, but the Association for the Study of Systematics in relation to General Biology is now engaged in revising taxonomic terms in all branches of biology.

Capt. C. DIVER. I fully agree with Dr Uvarov but would like to amplify his statement. The difference between varieties and subspecies is best considered on a genetic basis. The term "variety" we should apply to those cases where there is a single phenotypic difference from the type which is the product of a single gene or of a few genes acting together, whereas the term "subspecies" is only applicable to a group of organisms which differ from the type in respect of several more or less correlated genotypic changes. But these changes must be of a relatively minor nature which would not normally raise a sterility barrier and could not be regarded as a sound basis for specific distinction. These criteria must be considered also in relation to the way in which the different forms are distributed in natural populations. Varieties have a recognizable type of distribution which is to be expected from the nature of their genetic basis. They may form any percentage of any colony, and there may be several of them in the same colony. This, of course, is not true of the subspecies which will normally be distributed in relation to a region, though, as has been pointed out, there may be overlapping areas between two subspecies. The type of genetic difference which is recognized as subspecific is quite definitely a lower category than that of a species.

The Mollusca afford a few very good examples (e.g. *Cepaea*) of species with several geographical subspecies together with a number of varieties which are distributed through all the subspecies irrespectively. Of course, since evolution is still progressing, these distinctions cannot be absolute.

Dr A. R. CLAPHAM said that he thought it did not matter much to the ecologist exactly what status was given to a group by a taxonomist so long as the identification itself was correct.

Capt. C. DIVER. I do not agree with Dr Clapham that as long as the ecologist has got a name it does not matter to him what is the status of that name in the taxonomic hierarchy. It is of importance for him to know whether the systematist thinks what he has named is a species, a subspecies, or only a variety. And he should be able to test by the ecological relationships whether the work of the systematist is supported or not.

Mr CHARLES ELTON. (1) There is a need for deposited collections to back ecological surveys. Here the editor of a journal can exercise control.

(2) Community surveys cause ecologists to avoid taxonomic study, especially of animals, because of the large numbers of species concerned. This situation can be helped by (a) autecological studies embracing immediately related species, but not covering the whole field; (b) study of communities by taking only random species for intensive study, especially for transect investigations. The speaker has started to try this system in a long term study of a hawthorn-scrub hedge on chalk in Hampshire.

(3) The size of animals, e.g. size of species at sexual maturity or maximum size attainable, illustrates one junction of physiology (growth rates), ecology (size and growth affects population increase), and taxonomy (size of species). Such study involves laboratory observations on populations of the living animal, such as are being done now on rodents at Oxford.

Dr A. S. WATT. Information about the habitat on herbarium sheets is usually scrappy and sometimes misleading. Because the inorganic habitat is only one possible cause of species differentiation and because the likelihood of identifying the particular factor or complex of factors operative is remote, it is suggested that the best single criterion assessment of the total environment in which the species lives is to give the name or names of the plant communities in which it is found. This is so because the plant community integrates the inorganic environment and plant competition which must play an important selective part. The plant community is also an expression of the time factor. The speedy provision by the plant sociologist of diagnoses and a classification of plant communities is much to be desired.

Dr H. GODWIN. I am much impressed by the way ecologists tell taxonomists what they ought to do, and vice versa.

All the problems outlined serve to show the complexity of the issues involved. No unspecialized worker can hope to deal adequately with them—what is needed is the backing to finance a new type of worker to do this work specifically.

Nor is new nomenclature possible till the facts actually become known—nothing prematurely proposed can have permanency.

The PRESIDENT (Prof. TANSLEY, intervening in the discussion). It is not reasonable to expect a middle-aged systematist to train himself as a specialist in ecology, nor a middle-aged ecologist to become an expert systematist. Close co-operation between systematist and ecologist, which has been advocated by several speakers, is highly desirable; but it seems desirable to emphasize a point already made in introducing the subject, that the best results will be obtained by one and the same person working at vegetation from *both* sides. Undergraduates at the universities should be trained both in the *methods* of ecology and in those of systematy. Unless the student made a career of systematic botany he would probably never require the wide knowledge of the subject expected from the professional systematist. But he could quite well learn to apply modern taxonomic methods to the plants which were most important in the vegetation he was studying, e.g. the *Sphagna* of bog or "moss", or the fine-leaved fescues of dry semi-natural fernland instead of relying wholly on a specialist who might have little or no knowledge of ecology; and the knowledge so acquired would bring him much closer to the fundamental problems involved in the relation of species to the vegetation they composed.

Mr R. B. FREEMAN. Prof. Tansley has asked for a careful teaching of ecological and taxonomic principles in the university curricula. On this subject it was desirable to make a plea for the retention of a simple systematics. The speakers in the discussion have all emphasized the limitations of the present taxonomic method, and the ecologists have advocated a description embracing not only all the ecology that is already known, but also the physiology, cytology, genetics, and all other levels of organization. Such an unwieldy mass of data, though it may be the goal of some autecology, does not help the synecologist or the ecological beginner when they are confronted for the first time by a community with whose constituent species they are not familiar. It should be, as has already been stressed, part of the discipline of the autecologist to be familiar with the taxonomy of his own particular group. Among the woodlice, though there has been no general taxonomic study for 30 years, most of the species are critical and those that are not can be studied from the literature and the museum material. But when a zoologist comes to examine other animals closely bound up with the woodlice habitats, such as Phalangids and even spiders, he finds that there are no handbooks and very few specialist workers. The latter could, moreover, hardly be expected to name large masses of material.

If the taxonomists could produce a uniform series of handbooks containing accurate, brief, keyed morphological descriptions, with perhaps an average statement of life histories, and with indications of those species which require critical examination, both ecologists and taxonomists would be saved much time and labour. Mr Wilmott would probably object to the ecologist's naming the majority of his own material, on the ground that his eye will not be tuned

to recognize fine differences in what the handbooks call critical species; but even if taxonomic botany is so difficult as to make mathematical expression impossible, such a basis would allow the synecologist to proceed with some confidence and the beginner to begin.

Capt. C. DIVER. I am very glad Mr Freeman raised that point. It is extremely difficult for the animal ecologist to work at all widely if he has not got concise and practical handbooks on his groups. The Handbooks Committee of the A.S.S. are endeavouring to remedy this defect; the difficulty lies in getting the already overworked systematist to provide us with them. I personally regard it as a *sine qua non* that an animal autecologist should know at least the main species of his group before he starts to work, and that he should not burden the taxonomist with numbers of common species which he ought to be able to diagnose himself. But he should only send in those in critical groups on which he cannot be expected to express an opinion and which in any case the taxonomist himself will presumably wish to see.

Mr F. T. K. PENTELOW. One fundamental difficulty in the relation between ecology and taxonomy is that while accurate identification is essential, taxonomy continues to progress. Further taxonomy is purely subjective, and such concepts as species and variety have never been defined in scientific terms. The only solution is for ecologists to preserve all their material, no matter how well known they think it is, in order that it may be re-examined after further advances in taxonomy.

Dr W. B. TURRILL. The present symposium shows clearly that the time is ripe for closer co-operation between biologists working on more or less specialized subjects, and this is the main aim of the Association for the Study of Systematics. For example, the discussion has shown clearly the need for a complete collection of all terms used by biologists as group names. There are far more of these than generally realized, and they need very careful scrutiny and often precise re-definition. Mr A. J. Wilmott is collecting such terms for the Association, and ecologists are urged to help by communicating with him on the subject. It appears that there is often a general tendency for botanists and zoologists to use the same term with a different significance. Thus zoologists stress, at least in theory, obligatory sterility as a species criterion more than botanists do. They thus, on the whole, use ecological and geographical isolation much less than the botanist in separating species. The zoologist, judging from published theoretical accounts, considers what animals can and cannot breed together; the botanist is more inclined to emphasize what plants do and do not inbreed. There are exceptions to the above generalization and the botanist does not neglect sterility barriers, but they may be relatively less important in plants than in animals.

It is difficult to accept Mr Wilmott's view that there is a clear-cut difference between species (and subspecies) and variations due to simple gene differences. Combined taxonomic, genetical, and ecological studies on wild plants and wild populations show without doubt that every possible stage can be found from single gene to very numerous gene differences and from non-isolation to complete isolation.

Others who took part in the discussion were: Mr H. Baker, Mr H. Montford, Mr R. Ross, and Dr C. B. Williams.

ECOLOGICAL STUDIES ON THE RAIN FOREST OF SOUTHERN NIGERIA

II. THE ATMOSPHERIC ENVIRONMENTAL CONDITIONS

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(With thirteen Figures in the Text)

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I. INTRODUCTION

THIS paper, which forms part of the results of the Cambridge Botanical Expedition to Nigeria, will deal primarily with observations made on the rain forest environment near the Expedition's camp in the Shasha Forest Reserve in Southern Nigeria (for a detailed description of the situation, and of the

geology, climate, etc., of the district see Richards, 1939). The need for accurate information on environmental conditions in the undergrowth¹ of the forest became apparent in the course of the writer's investigations of the autecology of certain species of shrubs growing on the forest floor; as these studies were chiefly concerned with assimilation and transpiration, the factors measured were those directly affecting the aerial organs of the plant. Under expedition conditions it was found impossible to make adequate observations on the physiology of the plants, and specimens of the species investigated were therefore brought back to England in a Wardian Case for a more thorough study. Before work of this kind can be undertaken full information on the range of the various environmental conditions of the natural habitat is essential and measurements were therefore made in typical stations in the forest. Observations in tropical forests have previously been published by McLean (1919), Allee (1926), Carter (1934), Stocker (1935*a*, 1935*b*), von Faber (1935), and Moreau (1935), but the writer is not acquainted with any general review of environmental conditions in tropical rain forests, and comparisons of the present data with results from other parts of the world have accordingly been given.

The Expedition's camp was situated in the Shasha Forest Reserve near the village of Akilla. It was about 15 miles (24 km.) from the sea and lay within the belt of rain forest (here somewhat over 30 miles (50 km.) wide) which extends in varying width parallel to the coast from the Niger delta across Southern Nigeria towards Dahomey. The mean annual rainfall for 1921-34, recorded at Akilla, about 5 miles (8 km.) from the camp, is 2080 mm. (82 in.), and there is a dry season from December to February and a wet season from April to October, the remaining months being transitional (for a diagram of the seasonal distribution see Richards, 1939, p. 8). Nearly all the year round the prevailing wind is from the sea, and this probably has a profound effect in maintaining the humidity of the atmosphere during the dry season, as will be seen later. The factors which show the most marked seasonal changes are temperature and humidity, and in order to understand the changes in the environment of the undergrowth it was necessary to make observations on these factors in the canopy of the forest as well as in the lower layers. The observations were made at the end of the dry season (early March) and during the wet season (May). The atmospheric carbon dioxide concentration during the period March to May was also investigated, but no significant seasonal changes were observed. The observed seasonal changes in intensity of illumination in the shade were found to be small, as might be expected. However, in this evergreen forest the seasonal changes in light intensity are most likely to

¹ By undergrowth we mean the layer of undershrubs and occasional herbs reaching a height of about 1 m. in the primary forest ("herb layer" of Richards, 1939, p. 24). The 14- and 17-year-old secondary forest in which measurements were also made closely resembles the primary forest in respect of the structure of the lower layers. This secondary forest will be described by Mr R. Ross in a later contribution to these "Studies", which will also contain information on the temperature and humidity in the undergrowth of this type.

be caused by changes in sunfleck frequency with increased cloudiness in the wet season, and we have insufficient data of this on which to base any conclusions.

Except for the large and rapid local changes in intensity of illumination as sunflecks appear and disappear, environmental changes in the forest undergrowth are small and slow, in spite of the sparse vegetation. There is very little air movement except for the gusty period immediately preceding a thunderstorm, and as a result of the constancy of conditions it is easier to obtain a representative series of data on temperature, humidity, and carbon dioxide concentration in this than in almost any other terrestrial environment.

All times mentioned in this paper are some three-quarters of an hour fast of the sun, and sunset and sunrise are at about 6.45 and 18.45 respectively (the seasonal variation being insignificant). This is due to the use of Nigerian Standard Time.

The writer repeats the acknowledgements made in the previous paper in this series to all those whose interest and financial help made the Expedition possible, and also expresses his gratitude to the Director of the Royal Botanical Gardens, Kew, for the loan of a Wardian Case, to Dr W. R. G. Atkins, F.R.S., whose kind assistance was invaluable in the choice and calibration of the apparatus used for the observations of light intensity, and to Mr G. E. Briggs, F.R.S., for his helpful criticisms.

II. THE CARBON DIOXIDE CONCENTRATION IN THE UNDERGROWTH OF PRIMARY AND SECONDARY FOREST

It has been shown as a result of numerous investigations that the carbon dioxide content of the air in the lower layers of a temperate woodland is for a considerable proportion of the day higher than that outside the wood. A vigorous soil respiration has frequently been observed, and the structure of the wood must impede the mixing of the air near the soil with that outside the wood. In tropical rain forests, not only is there a vigorous decomposition (seldom is any continuous layer of dead leaves seen on the ground) but also the structure is much denser than that of most temperate woods. This led to the supposition that the carbon dioxide concentration in the lower layers of the former would be found to be much higher. This view was apparently substantiated by two observations made by McLean near Rio de Janeiro, giving a concentration of 0.14 vol. % in the evening and 0.34 early the following morning (the method used by McLean and the significance of his results will be discussed below). At the "normal"¹ concentration of carbon dioxide the rate of photosynthesis with a high light intensity increases almost proportionately with increasing carbon dioxide concentration. Even at low light intensities such as are met with in tropical rain forest a five- or tenfold increase in concentration would cause a large increase in the assimilation rate, and might be of importance in enabling plants to live under conditions of very low light

¹ We shall use "normal" concentration to signify a carbon dioxide content of 0.03 vol. %.

intensity. The term "carbon dioxide flora" has even been coined to describe these plants. von Faber (1935, p. 146) gives one of the most recent expositions of this view, and quotes some of his own observations in the mountain rain forest of Tjibodas in Java, giving values of from 0.082 to 0.096 vol. % of carbon dioxide in the day and 0.21 to 0.26 at night. These results are in marked contrast to those of Stocker (1935*a*), also made at Tjibodas, which we shall consider below. It will be shown that these measurements of very high concentrations are unsubstantiated, and that the concept of "carbon dioxide flora" is without foundation.

When the writer left England in December 1934 there were available in the literature only the two observations of McLean for tropical rain forest, and although these showed much higher concentrations than any which had been recorded from temperate woods, there was no *a priori* reason why this should not be so. When it was found that results of a different order were being obtained in Nigeria, further observations in the forest undergrowth were made, in order to explore the range of concentrations in this particular forest, especially in the early morning, when the highest concentrations were observed. Later Stocker's observations were published, suggesting that the concentration in tropical rain forest in general might be much lower than had been previously supposed, in spite of the additional observations of high concentrations published shortly before by von Faber. Stocker, in reviewing previous work, doubts the accuracy of both sets of observations of very high concentrations, but does not pursue the matter further.

(1) *Methods of measurement*

All the field methods for the measurement of carbon dioxide concentration with which the writer is acquainted depend on the absorption of the gas by alkali (usually baryta) and subsequent estimation of the alkali remaining. For this purpose it is necessary to have some form of aspirator which will take in a known volume of the air to be estimated, a vessel in which the absorption takes place and a titration or conductivity vessel. Numerous field methods have been described in which two or these three are combined, such as Lundegårdh's "Glockenapparat" (Lundegårdh, 1922), which combines aspirator and absorption vessel, and the more recent methods combining absorption and estimation vessels. Most of the results for tropical rain forest which we are discussing were, however, obtained by the simple method of combining all three in the form of a large bottle. This method is awkward in practice, but recommends itself when robustness and ready portability are important. Numerous precautions must be taken, however, if such a method is to give reasonably accurate results.

(a) *The writer's method.*

The carbon dioxide in a sample of air was absorbed by shaking with *N*/50 baryta in a bottle of about 5 l. capacity. The close-fitting cork, impregnated

with wax, carried two tubes. The lower end of tube *A*, through which the bottle was emptied of water, was flush with the surface of the cork. The tube *B*, which reached to the bottom of the bottle, served to fill it. The bottle, filled with water, was inverted, and a sample of air collected from the desired locality by a tube, usually 1 m. long, and with a capacity of about 25 ml., attached to *B*. The collection of a 4700 ml. sample took about 5 min. The collecting tube was held horizontally, so as to collect from one layer of air as far as possible. 25 ml. of approximately $N/50$ baryta were added through *B* and both tubes securely closed with rubber tubing and clips. The bottle was shaken for 25 min. and the air inside brought to atmospheric pressure through a soda-lime tube attached to *A*, care being taken that no liquid escaped; 25 ml. of carbon dioxide-free water were added through *A* to wash down any baryta which had collected there, the rubber tubing and clip were removed, and three drops of phenolphthalein introduced. The contents were titrated against $N/50$ oxalic acid, the burette having a piece of thin glass tubing, about 6 in. long, which in use passed right down tube *A* into the interior of the bottle, fastened on below the tap with rubber tubing. There was enough flexibility in the joint to allow of a gentle circulation of the contents of the bottle. As long as the full colour of the indicator remained, 0.5 ml. of acid could be added without danger of passing the neutral point. When neutrality was almost reached, 25 ml. of carbon dioxide-free water were added through *B*, washing down a little more baryta from it, the bottle detached from the burette, and a rubber tube and clip attached to *A*. The liquid was washed round the inside of the bottle, so as to collect the baryta from the sides and the underside of the cork. The titration was then completed and the contents poured out by *A*, a soda-lime tube being fixed to *B*. A further 25 ml. of baryta were then added, and the process of shaking and titrating as already described was repeated, the bottle being shaken for 15 min. It was found that if this whole procedure was repeated several times, there was no significant difference between the third and subsequent titrations. It was accordingly assumed that the absorption of CO_2 was complete at the end of the second shaking, and a standard practice was adopted of making three titrations in each estimation. The third of these was used as a blank value. If, however, several estimations were being made in one day, it was also assumed that the concentration of baryta did not vary during the day, and the blank value of the first estimation was used throughout. Consequently in subsequent estimations only two titrations were performed. A number of determinations have been made in the laboratory, since returning from Nigeria, on carbon dioxide in compressed air from a cylinder. Six determinations gave a fiducial value¹ for a single observation of 8.5 % of the carbon dioxide content.

¹ The fiducial value sets limits within which there is a 19 to 1 chance that the true mean of a hypothetically infinite population of observations would fall. It is derived by multiplying the standard deviation by the appropriate value of Fisher's "*t*" for the probability level 0.05.

(b) *Stocker's method.*

The method used by Stocker (1935*a*) is essentially similar. Air was drawn into the bottle, which lay on its side, by an aspirator operated from a distance of 2 m. It was assumed that the absorption of carbon dioxide was complete after a single period of shaking, and there was thus only one titration. This titration was completed after emptying the contents of the bottle into a flask. The first two of these differences tend to give too low a value for the carbon dioxide concentration, and the last one too high, but with careful manipulation the net effect of these will be small.

(c) *McLean's method.*

The following are the essential features of McLean's method (McLean, 1919) as described by him. "A five litre flask was fitted with a bung through which passed the tube of a 200 c.c. stoppered funnel. The flask was filled with water and 150 c.c. of a saturated solution of baryta was introduced into the funnel and the flask bunged. It was then removed to the forest and the water poured out slowly. . . . The baryta was then run into the flask from the funnel, and shaken about for 10-15 min. The flask was inverted, the stopcock of the funnel opened, and as much baryta as possible allowed to run back into the funnel. . . . Aliquot parts may then be pipetted off from the funnel and titrated against equal quantities of the original solution. . . . The acid employed was sulphuric, of such strength that 1 c.c. = 0.000614 g. or 0.312 c.c. of carbon dioxide.

"*Exp.* 1. The carbon dioxide in 5000 c.c. of air neutralized the baryta equivalent to 24.0 c.c. of acid = 0.14 c.c. % of air at N.T.P.

"*Exp.* 2. The carbon dioxide in 5000 c.c. of air neutralized the baryta equivalent to 59.25 c.c. of acid = 0.34 c.c. % of air at N.T.P."¹

It seems likely that this apparently high concentration of carbon dioxide was partly due to a dilution of the baryta by water left in the flask after most of the water had been poured out. To investigate the probable magnitude of this effect a very clean 5 l. flask was weighed, filled with water, emptied and shaken out. The flask was then inverted and allowed to drain, care being taken that no drop remained hanging at the top of the flask. The water retained after a definite period was measured by reweighing. This was repeated several times with different drainage periods, and it was found that with no drainage 7.7 g. was retained, and with 1, 2 and 5 min. 3.4, 2.7 and 1.8 g. respectively. We cannot say, of course, how much water remained in McLean's estimations, but it must have been at least 1.8 ml., and probably more, especially if the flask was not quite clean. A saturated solution of baryta contains 22.2 g./l. at

¹ On recalculation from the equivalence of the acid given, the concentrations are found to be 0.15 and 0.37 ml. at N.T.P. per 100 ml. of air at the temperature of the observation, respectively. If an N.T.P. correction were applied it would make these figures higher, probably about 0.16 and 0.40 vol. %.

10° C., rising to 35.8 at 20° C. and 41.9 at 25° C. No data for the temperature of the laboratory at the time that the solution was used are given, but from data for an earlier period in the year it seems likely to have been about 20° C., and it is more likely to have been higher than lower. The addition of 1.8 ml. of water to 150 ml. of a saturated solution of baryta at 20° C. produces a reduction of concentration equal to that caused by the absorption of the carbon dioxide in 5 l. of air containing 0.090 ml. % of carbon dioxide at N.T.P. Similarly, 3.4 ml. (1 min. drainage in our case) corresponds to 0.17 ml. %, and 7.7 ml. (no drainage) to 0.37 ml. %. In view of the magnitude and uncertainty of this error, it seems clear that no reliance can be placed on the results of McLean's method of determination.

(d) von Faber's method.

von Faber's technique and his series of observations do not appear to have been published in detail, and the writer has failed to obtain any information as to the method used; it is thus not possible to consider these further, other than to point out the discrepancy with the results of Stocker.

(2) Methods of expressing the results of estimations

It is possible to express the results of determinations of carbon dioxide concentration in various ways, and different authors have in the past used different forms, indeed in some cases the form used is not precisely defined. In Table I the writer's results have been expressed in several ways to facilitate comparison with the results of others. The numbering in the following note corresponds to the column headings in the table.

(a) The ratio of the volume of carbon dioxide to the volume of the permanent gases present is a useful measure, since it remains constant so long as no carbon dioxide is added or removed (the percentage changes of oxygen and nitrogen are negligible compared with the percentage changes in carbon dioxide).

(b) Figures for relative humidity are not available for all estimations; accordingly in this column the ratios of the volume of carbon dioxide to that of the total gas are given. It will be seen that in general they differ from the values in column *a* by about -3 % of the total content.

(c) If we are considering carbon dioxide as a reactant in a chemical process, its activity is required; assuming carbon dioxide to be a perfect gas this is best expressed as the partial pressure at the temperature of the estimation. The partial pressure is, of course, dependent on the temperature, barometric pressure, and the partial pressure of water vapour in the air.

(d) Other investigators have expressed their results in milligrams of carbon dioxide per litre of air estimated, some correcting the volume to N.T.P., others not doing so. For comparison with these results, figures for weights of carbon dioxide per litre of air under the conditions of the estimation are also given.

(3) *Observations in Nigeria*

The complete results of all the estimations which were made in primary and secondary forests are given in Table I, under the headings which refer to the

Table I. *Carbon dioxide concentrations at stations in the Shasha Forest Reserve, Southern Nigeria, during 1935*

Columns refer to methods of evaluation on p. 442.

Date	Time	a %	b %	c mm.	d mg./l.
(1) 0.6 m. above ground in primary forest, near the Odoko tree mentioned on p. 448.					
2. iii.	9.35	0.057	0.055	0.42	0.98
6. iii.	10.27	0.043	0.042	0.32	0.75
(2) 0.3 m. above ground in primary forest, near sample plot 2 of Richards (1939, p. 56).					
2. v.	7.55	0.058	0.057	0.43	1.04
	11.15	0.043	0.042	0.32	0.75
	12.55	0.040	0.039	0.30	0.71
	14.45	0.042	0.041	0.31	0.75
3. v.	7.40	0.042	0.041	0.31	0.75
	9.30	0.051	0.050	0.38	0.90
	11.50	0.037	0.036	0.27	0.65
4. v.	7.45	0.049	0.048	0.37	0.86
(3) 1.2 m. above ground, in 17-year-old secondary forest continuous with sample plot III of Ross (forthcoming contribution to these "Studies").					
13. iv.	8.15	—	0.053	0.40	0.96
15. iv.	7.05	—	0.053	0.40	0.96
	10.00	—	0.045	0.34	0.81
	13.35	—	0.033	0.25	0.59
	16.30	—	0.033	0.25	0.59
16. iv.	7.00	—	0.044	0.34	0.79
17. iv.	7.10	—	0.050	0.38	0.90
30. iv.	12.20	—	0.038	0.29	0.67
14. v.	7.10	—	0.052	0.40	0.94
17. v.	7.00	—	0.054	0.41	0.98
18. v.	7.25	—	0.047	0.36	0.84
22. v.	7.05	—	0.055	0.42	0.98
23. v.	7.05	—	0.058	0.44	1.04
(4) 1 m. above ground in a swamp dominated by Aroids, similar to that shown by Richards (1939, Pl. II, phot. 4).					
18. iv.	7.20	—	0.059	0.45	1.08
	11.10	—	0.039	0.30	0.69
	16.40	—	0.041	0.31	0.73
(5) 0.4 m. above ground, in the open in a young Kola plantation.					
11. iii.	9.10	0.035	0.034	0.26	0.60

methods of evaluation given above. The table also gives the date and time of the readings. Fig. 1 shows the values given in column *b* plotted against time of day, the points for primary and secondary forest being distinguished from each other. It is apparent that there is no significant difference between the two types over the period of this investigation.

The highest concentrations are observed in the early morning, the mean of seven determinations during the half-hour after sunrise being 0.052 vol. %, while that of seven made after 11.00 is 0.037. It will be noticed that all the twenty-three observations lie between the "normal" concentration of 0.03

vol. % and twice "normal". The fall in concentration during the day is probably not wholly due to the assimilation of the plants, but also to the increased mixing of the forest air with the outside air caused by the greater wind in the forenoon and convection currents due to sunflecks. This fall during the day has been observed by numerous workers on European woods. (Stocker (1935*a*) has reviewed this work and compared it with his data for forest at Tjibodas in Java.)

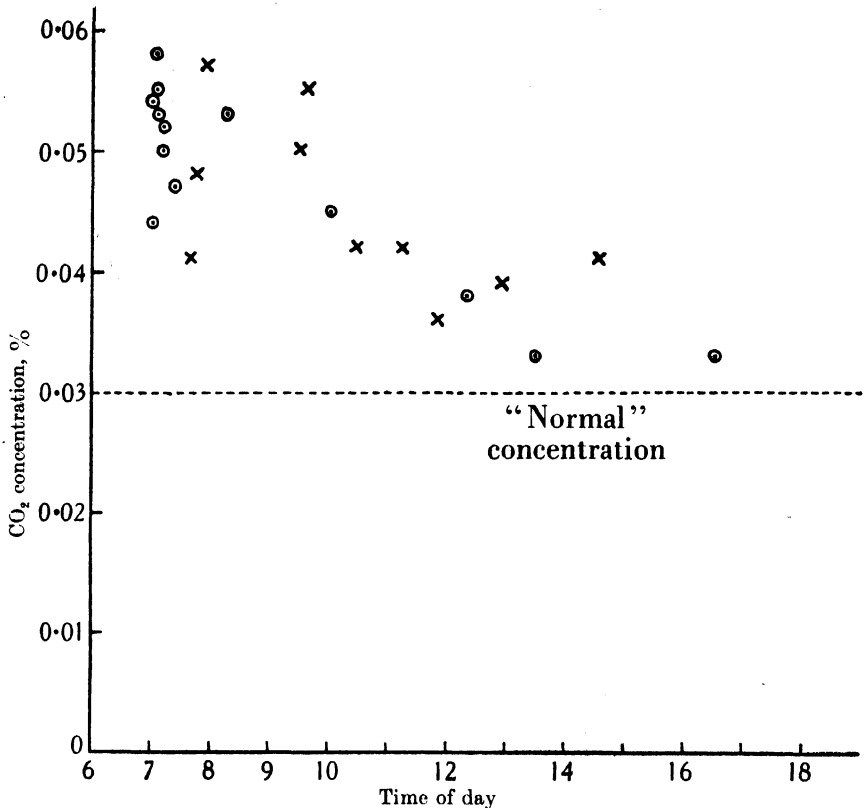


FIG. 1. Carbon dioxide concentration in undergrowth in the Shasha Forest Reserve, Southern Nigeria. For details see Table I and text, p. 443.

x primary forest.

o secondary forest.

Table I also contains for completeness the results of three estimations made in the dense undergrowth of an open swamp very similar to that figured by Richards (1939, Pl. II, phot. 4), and it will be seen that the concentrations here are of the same order as those in the forest. There is also included a single observation of the concentration in the open, in a plantation of Kola in the middle of a large cleared area of land; the stand was a very open one, the trees being young, about 3 m. in height. They were spaced as in an orchard, and there was a ground cover of weeds varying in height up to about 1 m. The

concentration here is significantly lower than any of the observations made in the forest at the same time of day, and is not appreciably different from the "normal" concentration in open air.

(4) *Comparison with Stocker's observations at Tjibodas, Java*

Stocker (1935a) carried out observations over a period of three days at Tjibodas in Java. Fifteen sets of three parallel observations were made, one 1.5 m. above the lawn in front of the new Treub laboratory, one 0.07 m. above the ground in a small wooded valley behind the guest-house, and one 1.7 m. above the ground in the fork of a 15 m. Sauraja tree. The values of carbon dioxide concentration, expressed as mg./l., are plotted against time of day in Fig. 2 for the last two named positions.¹

It will be noticed, first, that the values are lower than those found by the writer in Nigeria. Only one value exceeds 1.5 times "normal", while of the observations at 1.7 m., 10 points are below "normal" as against (3) above; none of the writer's observations was below "normal". Secondly, there is a marked rise in concentration, in both situations, between 6.30 and 8.45. This lower concentration is established by six observations in the early morning, while there was no trace of this in the writer's data (the reader will remember that mean sunrise in Nigeria is at 6.45, as against 6.00 for Buitenzorg). From 9.00 onwards, however, there is a fall similar to that found in Nigeria.

In comparing the two sets of data the difference in the type of forest concerned must be noted. The Nigerian rain forest is in part primary and in part secondary forest similar to it in essential physical characteristics, such as mean temperature, shading, and absence of dew at night. On the other hand, the rain forest in which Stocker's work was carried out was a mountain type (1300 m.), and the temperature near the forest floor was about 9° C. or more lower than in Nigeria. Furthermore, the place at which the observations were made was very open, with a dense growth of epiphytes, a state of affairs possible in Nigeria at a height of 1.7 m. only in clearings, on the sites of fallen trees, etc. The openness of the whole forest is shown by the heavy dew within the forest at night; in Nigeria it was very noticeable that dew ended sharply at the edge of the forest, there being a heavy dew in clearings but none in the forest undergrowth, a point which will be referred to again later.

There are two principal differences between Stocker's data and those of the writer; the former are generally lower, and show remarkably low values in the early morning. We have already seen that there may be systematic errors in the method of estimation, but that these are likely to be small. Further, the Tjibodas forest being more open, these values would be expected to approximate more closely to the carbon dioxide content of the outside air. The mean

¹ Stocker nowhere states whether litre of space estimated, or litre of air at N.T.P. is meant. Elsewhere in the same paper, however, he gives the equivalence 0.56 mg./l. = 0.028 vol. %, which indicates air at N.T.P. It is not clear whether a correction has been made for water vapour or not.

of the values for "open air" recorded by Stocker is 0.51 mg./l., as against a "normal" content of 0.59, suggesting that the air near this forest may in general have a much lower concentration than is usually met with, due to edaphic or other causes. This suggestion is partly substantiated by the mean of about 120 air analyses made by Stocker in the Buitenzorg gardens using an independent method, which gave a figure of 0.56 mg./l. This, although higher than the Tjibodas result, is nevertheless lower than the "normal" of 0.59.

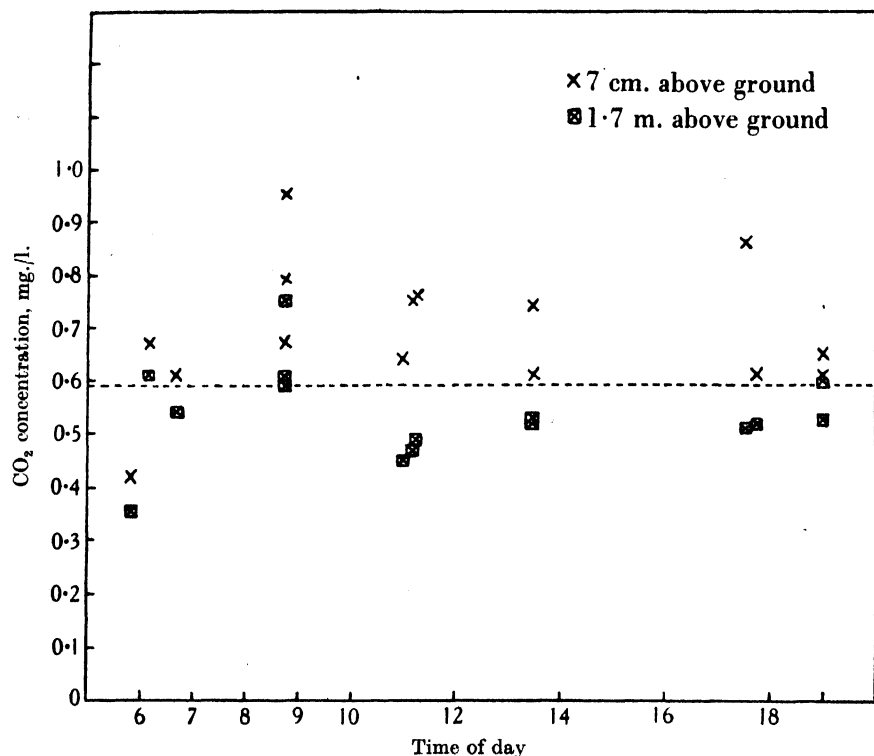


FIG. 2. Stocker's observations of carbon dioxide concentration at Tjibodas in Java.

The dotted line represents "normal" concentration. For explanation see text, p. 445.

Stocker takes the view that these low values are characteristic of tropical rain forest in general, but as we have seen the writer's results do not confirm this view.

Turning now to possible explanations of the six low values recorded between 5.50 and 6.40, we find that Stocker assumes also a fall in concentration in the evening, though Fig. 2 shows that there is no justification for this, particularly in the data for 1.7 m. To explain both the morning and the supposed evening fall of concentration he puts forward a hypothesis of "binding" of carbon dioxide in the evening and during the night, followed by a sudden rise of concentration in the early morning as the "bound" carbon dioxide becomes free. He suggests that this may have a connexion with dew, but, realizing that

solution in water alone would not account for the magnitude of the phenomenon, he further suggests, on a basis of observations by Arens (1934) on the high pH of dew drops on leaves, that carbon dioxide is absorbed by this alkali and liberated again on the evaporation of the dew in the early morning. Bearing in mind that the only phenomenon which has to be explained is the rise in the early morning, it is apparent that the only way in which such a mechanism could work is by the absorption of carbon dioxide by a solution of a carbonate to form a mixture of carbonate and bicarbonate, from which the carbonate is redeposited on evaporation with the evolution of carbon dioxide. The only carbonates which are likely to be concerned in this postulated process are those of potassium, sodium, and calcium, and of these calcium may be eliminated at once, as owing to the low solubility of the CaCO_3 , $\text{Ca}(\text{HCO}_3)_2$ system at least a thousand times as much dew as we should expect would be required to account for the observed rise in carbon dioxide content of the air. Of the two alkali metals, the system $[\text{NaHCO}_3, \text{Na}_2\text{CO}_3, \text{CO}_2, \text{H}_2\text{O}]$, in equilibrium with "normal" carbon dioxide concentrations, does deposit sodium carbonate on evaporation, giving off carbon dioxide in the process (see data in *International Critical Tables*, 4, 299, and Walker *et al.* (1927)); the writer has been unable to find any similar information in regard to the potassium salts, but for a quantitative examination of the hypothesis we may assume that the same holds as for sodium. Of course, if the bicarbonate is deposited instead of the carbonate, the system will take up carbon dioxide as it evaporates, and this possible mechanism would have to be rejected as it would work in the wrong direction. It is a simple matter to calculate how much carbonate and dew would be required to absorb and give off again on evaporation the observed increase of 0.192 g. per cubic metre in the carbon dioxide content of the air (the following estimates are based on data in Walker *et al.* (1927)). It will be seen that these estimates are minimal ones, as mixture with air outside the forest would be causing a continual reduction in the concentration inside, at least in the later stages of the rise. Assuming the solutions to be saturated, we find in the case of sodium that 26 g. of $\text{Na}_2\text{CO}_3 \cdot 10\text{H}_2\text{O}$ dissolved in 39 ml. of dew per cubic metre of air would be needed, and in the case of potassium the corresponding figures are 18 g. of K_2CO_3 dissolved in 17 ml. of dew. Such quantities of carbonates per cubic metre of air are not likely to be accounted for by the small traces observed by Arens on leaves, and so much deposit on the surface of the foliage could not fail to attract attention. Furthermore, on a basis of the known cooling of the air near ground-level we should expect 3 ml. of dew per cubic metre of air, and although this quantity would probably be somewhat exceeded owing to the foliage being colder than the air, yet the total water content of a cubic metre of saturated air under these conditions (16 g.) is less than either of the postulated amounts of dew. If we assume the solutions to be more dilute less carbonate is required to absorb the same amount of carbon dioxide, but at the same time the dew needed to dissolve the carbonates

increases; for example, if the final solutions are centinormal, we require only 1.5 g. of $\text{Na}_2\text{CO}_3 \cdot 10\text{H}_2\text{O}$ or 0.7 g. of K_2CO_3 per cubic metre, but in both cases 1.1 l. of dew are required.

It seems on these grounds, then, that we must reject Stocker's hypothetical system as the primary cause of the early morning rise in carbon dioxide concentration, though it is true that it might be a minor contributory factor to a rise due to some other cause. In the absence of further information the phenomenon is not readily explained. After a consideration of various possibilities the writer concluded that the most likely explanation is that the surface soil being cooled by radiation during the night (witness the dew), there is a mass flow of air into the pores, slowing up the outward diffusive movement of carbon dioxide. On the reversal of this mass flow, following on the warming of the upper layers of the soil after sunrise, carbon dioxide would be given off more rapidly. There is, however, no information available on the respiration and physical characters of the soil in forests such as those at Tjibodas or in the Shasha Reserve, and no information on the fall in soil temperature in either case, though it is probably considerably less in the latter. The probable magnitude of this effect cannot be estimated.

III. TEMPERATURE AND HUMIDITY IN THE UNDERGROWTH AND TREE TOPS OF PRIMARY FOREST

In this section we shall consider the conditions of temperature and humidity in the undergrowth of primary rain forest, and also those in a position above the main canopy near one of the undergrowth stations. The data for the latter are not only interesting in themselves but also shed light on the causes of some of the changes in the former habitat. In the undergrowth a set of instruments was placed on a shelf at a height which on different occasions varied from 0.6 to 0.8 m. above the ground under a small roof, arranged not to interfere with ventilation while affording protection from rain and direct sunlight. When simultaneous observations were being made a second set was placed in a shelter, also arranged to keep off rain and direct sunlight, while allowing unhindered ventilation; this was fixed at a height of 23.8 m. to a branch of an Odoko tree (*Scotellia* sp. near *kamerunensis*) whose base was about 10 m. from the undergrowth instruments. This tree was about 28 m. high. The densest layer of the vegetation in the neighbourhood was a mass of third-storey trees between 9 and 12 m., and above 11 m. it was possible to see on all sides, as may be seen in the view from this tree which is given by Richards, 1939, Pl. II, phot. 3. This structure appears to be typical of the primary forest in this district, as may be seen by comparison with the sample plots described in detail by Richards (1939, Fig. 4 and text). Records were obtained during the dry and at the beginning of the wet seasons.

Bimetallic strip thermographs and hair hygrographs were used. The instruments in the tree were reached by a rope ladder, and the charts of both

sets were changed every evening. At the same time both hygrographs were adjusted from the reading of a whirling hygrometer; the thermographs were found to remain correct for the duration of one set of records, which usually lasted for about a week. It will be well before considering the data themselves to make a few remarks on the behaviour of the recording instruments when working under tropical rain-forest conditions.

(a) In a very wet atmosphere, there is a tendency for the recorder ink to spread over the chart, and make a very thick line, extending sometimes over as much as 1°C . or 2 %. This effect is most marked in charts which are exposed for the longest time to high humidities—the forest undergrowth records, and in particular those for the wet season. This causes some uncertainty in estimating the position of the original line. It is, however, responsible for only a small error, which is not likely to exceed 0.2°C . or 0.5 % in the worst cases.

(b) Hair hygrographs tend to be inaccurate above about 90 % to such an extent that individual readings above 93 % cannot be considered as significantly different from saturation. They may, however, be so considered if they occur on a record only a short time before or after a period of higher record, and if the whirling hygrometer readings taken at the beginning and end of the chart do not indicate any serious deviations from the correct setting.

(c) Hair hygrographs almost always deviate more or less from the correct setting during the period of a record. This deviation tends to be slight when there are only slight changes in the relative humidity during the period of the record, particularly if the period has been preceded by a previous exposure to very similar conditions. Hence the readings from the instruments in the undergrowth rarely involve large errors due to this cause. In the case of the instruments in exposed positions, however, where there is a large change in relative humidity during the day, the changes in setting may be considerable, and some sort of allowance must be made for them in an interpretation of the chart. The simplest basis for correction is the assumption that the deviation from the correct setting has been progressive and regular during the day, but this is open to the obvious objection that a large change may have taken place in a short period, and have been followed by a slower change. An error of 1 or 2 % may thus easily be present in the readings from such a chart.

(1) *General comparison of records for dry and wet seasons*

Tables II–V, derived from readings of the charts, give the maximum and minimum temperatures, daily range of temperature, and maximum and minimum relative humidity for the days shown. Low values of relative humidity were occasionally recorded in the undergrowth for very short periods of about 5 min., being presumably caused by puffs of wind. Hence the absolute minimum on the chart is probably of little biological significance for the plants in the undergrowth, as the effect of a low humidity for so short a time on the

*Rain Forest of Southern Nigeria*Table II. *Temperature and humidity in top of Odoko tree, 23.8 m. above ground-level*

Date	Max. temp. ° C.	Min. temp. ° C.	Daily range of temp. ° C.	Max. R.H. %	Duration of max. R.H. hr.	Min. R.H. %	"Half- hour min." R.H. %	Daily range of R.H. %
5. iii.	35.0	24.9	10.1	95	11	62	63	32
6. iii.	35.3	24.7	10.6	100	12	63	65	35
7. iii.	34.8	25.6	9.2	100	10	66	67	33
8. iii.	35.0	25.0	10.0	100	9	57	60	40
9. iii.	33.0	24.0	9.0	95	11	60	62	33
10. iii.	31.4	20.7	10.7	95	12	64	66	29
11. iii.	33.0	23.0	10.0	98	12	60	64	34
Mean	33.9	24.0	9.9	97.6	11.0	61.7	63.9	33.7
9. v.	32.1	22.0	10.1	95	10	64	66	29
10. v.	28.9	20.2	8.7	95	10	71	73	22
11. v.	31.1	21.3	9.8	94	12	64	67	27
12. v.	32.2	22.0	10.2	95	11	52	55	40
13. v.	28.0	22.2	5.8	95	12	77	79	16
14. v.	30.4	21.4	9.0	95	12	63	65	30
15. v.	30.3	22.6	7.7	95	11	60	62	33
16. v.	34.4	21.9	12.5	95	11	65	68	27
Mean	30.9	21.8	9.2	94.9	11.1	64.5	66.9	28.0

Table III. *Temperature and humidity in primary forest 0.7 m. above ground, below tree-top recorder*

Date	Max. temp. ° C.	Min. temp. ° C.	Daily range of temp. ° C.	Max. R.H. %	Duration of max. R.H. hr.	Min. R.H. %	"Half- hour min." R.H. %	Daily range of R.H. %
5. iii.	29.8	24.8	5.0	93	14	70	75	18
6. iii.	31.0	24.4	6.6	97	14	68	75	22
7. iii.	30.0	24.8	5.2	91	12	65	74	17
8. iii.	30.4	24.0	6.4	97	13	70	74	23
9. iii.	29.7	24.4	5.3	95	12	66	74	21
10. iii.	27.9	21.0	6.9	95	18	72	86	9
11. iii.	29.2	23.7	5.5	95	16	70	78	17
Mean	29.7	23.9	5.8	94.7	14.1	68.7	76.6	18.1
9. v.	27.8	24.0	3.8	95	14	82	88	7
10. v.	25.8	22.0	3.8	95	20	89	92	3
11. v.	26.1	23.0	3.1	97	18	90	94	3
12. v.	26.9	23.4	3.5	97	19	86	93	4
13. v.	25.8	23.8	2.0	97	22	95	96	1
14. v.	26.8	23.0	3.8	97	18	88	93	4
15. v.	27.4	23.9	3.5	97	17	89	93	4
16. v.	28.0	23.3	4.7	95	14	80	88	7
Mean	26.8	23.3	3.5	96.2	17.8	87.4	92.0	4.1

transpiration will be negligible. Accordingly the minimum value of relative humidity recorded either continuously for half an hour, or discontinuously for periods totalling half an hour, is given in the tables (*half-hour minimum*) as well as the absolute minimum. In the undergrowth the former value is usually about 5-10 % higher than the latter, in the tree tops about 2 %. The "half-hour minimum" is used as a basis for the calculation of the daily range of

Table IV. *Temperature and humidity 0.7 m. above ground, in primary forest in the same position as that referred to in Table III*

Date	Max. temp. ° C.	Min. temp. ° C.	Daily range of temp. ° C.	Max. R.H. %	Duration of max. R.H. hr.	Min. R.H. %	"Half- hour min." R.H. %	Daily range of R.H. %
22. ii.	29.0	22.6	6.4	95	14	73	76	19
23. ii.	25.8	19.5	6.3	94	13	87	87	7
24. ii.	27.9	21.1	6.8	97	22	93	96	1
25. ii.	29.2	23.1	6.1	95	18	77	86	9
26. ii.	28.8	23.2	5.6	—	17	—	—	8
27. ii.	29.7	—	—	95	—	74	80	15
28. ii.	30.0	24.0	6.0	92	17	65	78	14
1. iii.	29.9	24.7	5.2	95	17	79	85	10
2. iii.	30.2	24.5	5.7	91	17	73	78	13
Mean	28.9	22.8	6.0	94.3	16.9	77.6	83.3	10.7

Table V. *Temperature and humidity 0.7 m. above ground, in primary forest on the edge of sample plot 2 of Richards (1939)*

Date	Max. temp. ° C.	Min. temp. ° C.	Daily range of temp. ° C.	Max. R.H. %	Duration of max. R.H. hr.	Min. R.H. %	"Half- hour min." R.H. %	Daily range of R.H. %
1. v.	25.1	21.8	3.3	95	21	86	92	3
2. v.	27.6	22.3	5.3	92	17	83	88	4
3. v.	27.0	22.4	4.6	95	20	88	92	3
4. v.	26.4	22.8	3.6	96	23	90	95	1
5. v.	27.0	22.8	4.2	97	22	94	94	3
6. v.	27.6	21.3	6.3	96	22	84	91	5
Mean	26.8	22.2	4.6	95.2	20.8	87.5	92.0	3.2

Table V refers to a 24 hr. period beginning at 9.00 on the date given, and ending at 9.00 on the following day.

Tables II, III, IV and VI refer to a 24 hr. period beginning at 17.00 on the day previous to the date given and ending at 17.00 on that date.

relative humidity given in the tables; the duration of the maximum relative humidity (which does not differ significantly from saturation) in hours is also given. The principal data which we shall consider later in greater detail are those in Tables II and III, which refer to periods when simultaneous records were being made in the undergrowth and in the tree tops. Tables IV and V give additional observations, Table IV referring to the same spot in the undergrowth near the Odoko tree at an earlier period than the observations given in Table III, while Table V gives data for a station near sample plot 2 of Richards (1939), very close to the spot where the determinations of carbon dioxide concentration given in Table I (2) were made.

The general conclusions which can be drawn from these tables are as follows:

(a) Comparing the data for the undergrowth with the tree-top data, we see that, in the dry season

(i) the maximum temperature is about 4° C. lower in the undergrowth, but the minimum temperature is about the same,

(ii) the "half-hour minimum" of relative humidity is about 15 % higher in the undergrowth, and thus the daily range is reduced to half,

(iii) the duration of the maximum relative humidity is from 4 to 5 hr. longer in the undergrowth.

(b) In the wet season, these differences are much accentuated, and further, the minimum temperature on the forest floor is in every case from 1 to 2° C. higher than in the tree tops. We shall see later, when considering particular days in greater detail, that on the day chosen as representative of the wet season the lower temperature in the tree tops at night is reached by a steady fall going on until sunrise, whereas on the chosen day in the dry season there was little fall after 1 a.m. The lag in the cooling of the undergrowth may thus in part be responsible for the minimum temperature on the forest floor being higher than in the tree tops.

(c) In the undergrowth, the chief differences in passing from the dry to the wet season are

(i) a lower maximum temperature, the minimum remaining approximately the same,

(ii) a higher minimum humidity,

(iii) a longer duration of the maximum relative humidity.

(d) In the tree tops, however, in passing from the dry to wet season we notice that

(i) both maximum and minimum temperature are from 2-3° C. lower, the daily range not being significantly different,

(ii) there are not sufficient data to say whether there exists a significant difference in relative humidity, though there is an indication of such a difference,

(iii) the duration of maximum relative humidity is almost identical.

(2) Detailed comparison of selected days

For autecological purposes much more detailed information than that so far discussed is desirable, especially in a tropical rain-forest climate where the extremes of temperature and humidity are probably well within the limits of tolerance of the species concerned. The form of the daily march of temperature and humidity is important, and a set of maxima and minima such as we have just considered tells us little in regard to this. A more detailed treatment of the daily records will also give a clearer insight into the nature of the seasonal changes and of the relation between conditions in the canopy and the undergrowth. Such a treatment might be presented without undue detail either by giving the weekly mean conditions at, say, hourly intervals in a particular situation, or by considering only one day in each situation. Although the first method is preferable on general grounds as giving a picture more free from the idiosyncrasies of a particular day, yet, owing to the imperfections in the charts mentioned above, it is doubtful whether we should achieve a better representation of conditions in general which would compensate for the greatly increased

labour of the analysis. Indeed, it seems preferable rather to present the data for the days for which comparatively accurate records are available, than to mix them up with others more imperfect. An examination of the records showed that it was fortunately possible to select from the best charts days whose conditions of temperature and humidity, both for the canopy and the undergrowth, approximated closely to the means of the periods from which they were taken. Table VI gives a comparison between the weekly mean and the particular day selected as typical, under the headings already considered.

Table VI. *Temperature and humidity in primary forest, showing a comparison of the mean conditions during a period (a) with the conditions on the day taken as typical of the period (b).*

		Max. temp. ° C.	Min. temp. ° C.	Daily range of temp. ° C.	Max. R.H. %	Duration of max. R.H. hr.	Min. R.H. %	"Half- hour min." R.H. %	Daily range of R.H. %
Dry season									
Tree top:	(a)	33.9	24.0	9.9	98	11	62	64	34
	(b)	33.0	24.0	9.0	95	11	60	62	33
Undergrowth:	(a)	29.7	23.9	5.8	95	14	69	77	18
	(b)	29.7	24.4	5.3	95	12	66	74	21
Wet season									
Tree top:	(a)	30.9	21.8	9.2	95	11	65	67	28
	(b)	31.1	21.3	9.8	94	12	64	67	27
Undergrowth:	(a)	26.8	23.3	3.5	96	18	87	92	4
	(b)	26.1	23.0	3.1	97	18	90	94	3

(a) *The daily march of temperature and humidity.*

A very convenient method of presenting a great deal of information on diurnal changes of temperature and humidity in a simple and convenient form was adopted by Buxton & Lewis (1934). Using means from a number of successive charts, they plotted the temperature at a particular time against the relative humidity at the same time at 2-hourly intervals throughout the day. They thus obtained a series of points which when joined gave a closed polygon representing the diurnal march of both temperature and relative humidity. They were also able to follow the march of saturation deficit (vapour pressure deficit in millimetres of mercury) on the same graph by adding a set of lines of constant saturation deficit (i.e. lines showing the relation between relative humidity and temperature when the saturation deficit remains fixed at any given value). The method of analysis which we shall use below is essentially similar to this: as we are using data for a single day and not the mean of a period the polygon we obtained is not closed, except by accident. We have plotted the temperature as the independent variable, as abscissae instead of ordinates, and added a further family of lines to the graph, lines of constant absolute humidity (expressed as vapour pressure). These enable us to obtain information on any changes which may be taking place in the water

vapour content of the air due to transpiration, mixing with drier air, deposition of dew, or other causes. Thus on one graph we may examine and compare the daily march of temperature, relative humidity, saturation deficit, and water vapour content of the air, and observe any correlations between them.

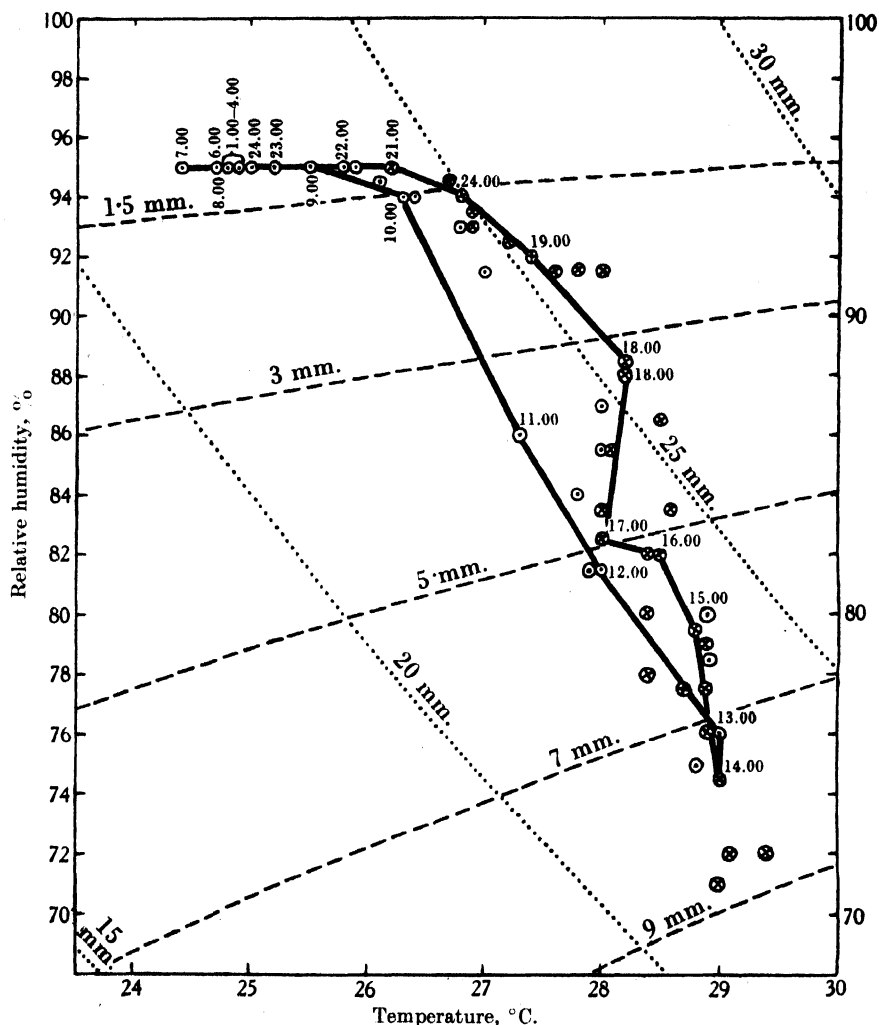


FIG. 3. Temperature and relative humidity in the undergrowth of primary forest in Nigeria, 8-9. iii. 35. For explanation of "grid" lines see text, p. 453.

In Figs. 3-6 are plotted the data for the two days from 18.00 on the 8th to 18.00 on the 9th day of March, and from 18.00 on the 10th to 20.00 on the 11th of May (the extra two hours bring us back approximately to the position at 18.00 on the 10th, when the sky was much more overcast). The readings were taken from the records at hourly intervals, and these are joined by straight lines. In order to give some idea of the extent of the fluctuations, which may

in part be real, and in part be due to experimental errors, readings have been taken from the records during the day at quarter-hourly intervals and plotted as isolated points. Any attempt to join these up merely results in confusion unless a very large scale is used, but the points before and after noon have been distinguished from each other by being plotted as circles with dots and crosses inside them respectively. In these and the subsequent figures of the

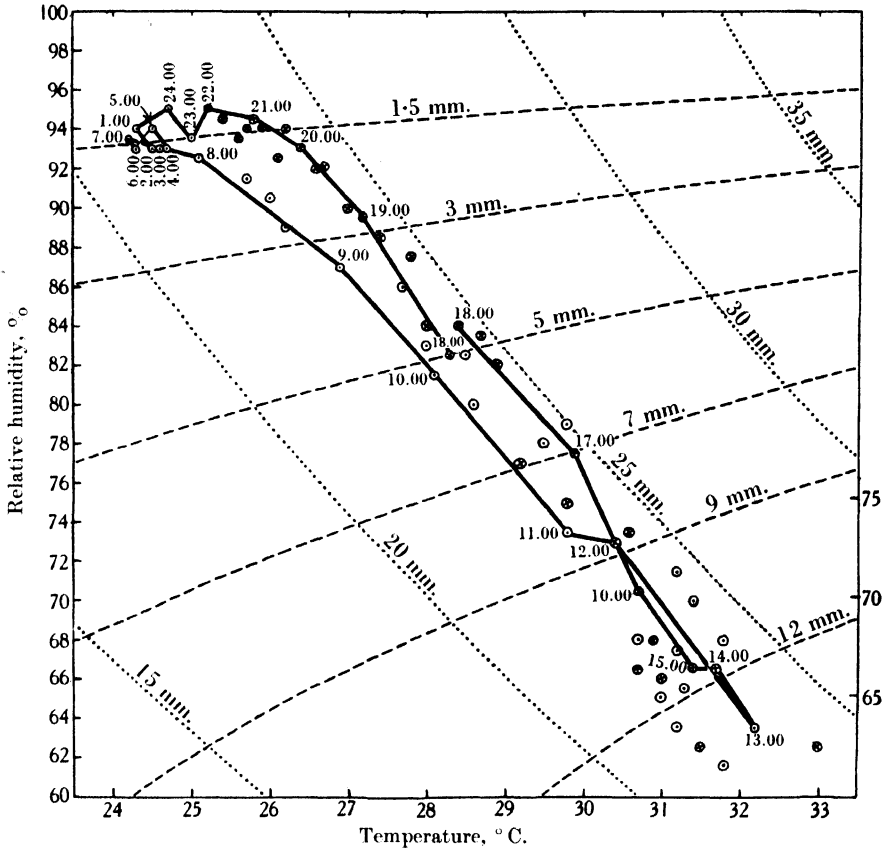


FIG. 4. Temperature and relative humidity at 23.8 m. in the canopy of primary forest in Nigeria, 8-9. iii. 35.

same type (Figs. 9-11) the family of lines of constant saturation deficit are represented as broken lines, and those of constant vapour pressure as dotted lines, marked with the appropriate value in millimetres of mercury of the saturation deficit or vapour pressure respectively.

The relatively small air movements in the undergrowth of primary forest suggest that the conditions obtaining there might be compared with those in a closed system containing water and water vapour. If we consider such a system, in equilibrium, the temperature of which is being raised, and plot the relative humidity against the temperature, we find that the former remains at

100 % until all the water has evaporated, and then follows approximately one of the family of lines of constant vapour pressure. The departure from this relation will be negligible for the small temperature changes with which we are dealing (in this region it is about $+0.32\%$ per $^{\circ}\text{C}.$). If we consider further a system of an aqueous solution and water vapour we find that, starting at a relative humidity corresponding to the vapour pressure of the solution at the

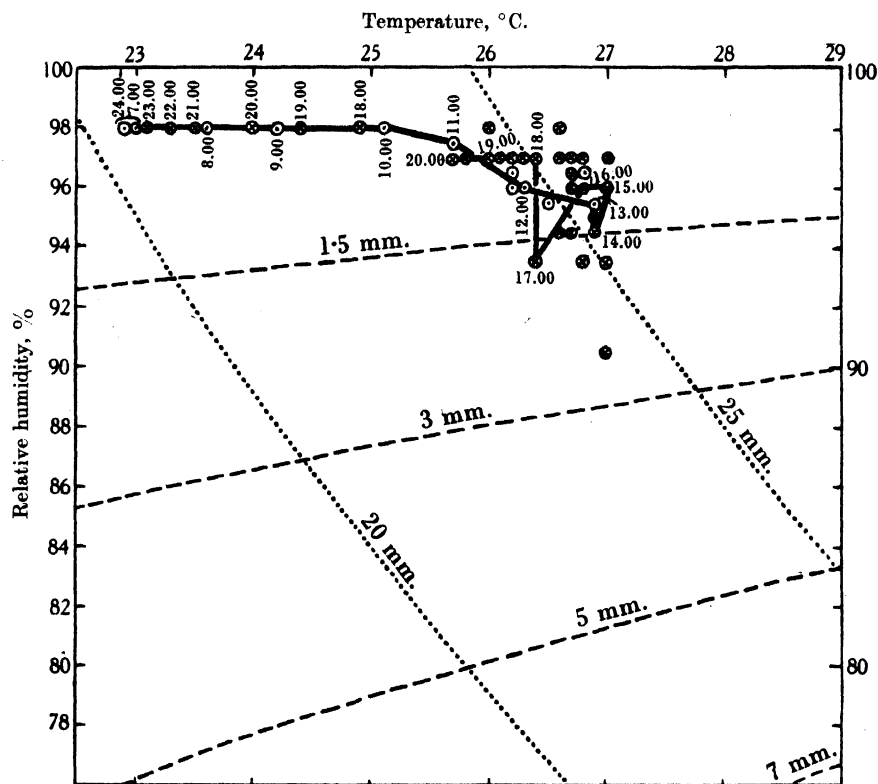


FIG. 5. Temperature and relative humidity in the undergrowth of primary forest in Nigeria, 10-11. v. 35.

initial temperature and concentration, as the temperature is raised, water will evaporate, the solution will become more concentrated, and the relative humidity will fall until the solution is saturated. The curve will then enter on a new phase of slow rise, fall, or constancy of relative humidity, depending on the properties of the saturated solution in question, until all the water has evaporated, when it will again follow approximately one of the lines of constant vapour pressure, as in the simpler case. If, as under natural conditions, the system is not in equilibrium, there will be a lag in evaporation or condensation, the relative humidity will fall below, or rise above, the equilibrium value as the system is heated or cooled, and the distinction between the various phases of the curve will be obscured. There appears to be evidence of hysteresis in

Figs. 3, 4 and 6. The quarter-hourly readings in the morning before 10.00 (circles and dots) all show a lower vapour pressure than the evening points (circles and crosses) after 18.00, which lie close to them.

Little can be concluded from Fig. 5 for the wet season in the undergrowth, as the daily range is so small compared with the random fluctuations: however, the last relation discussed above forms a close approximation to observation

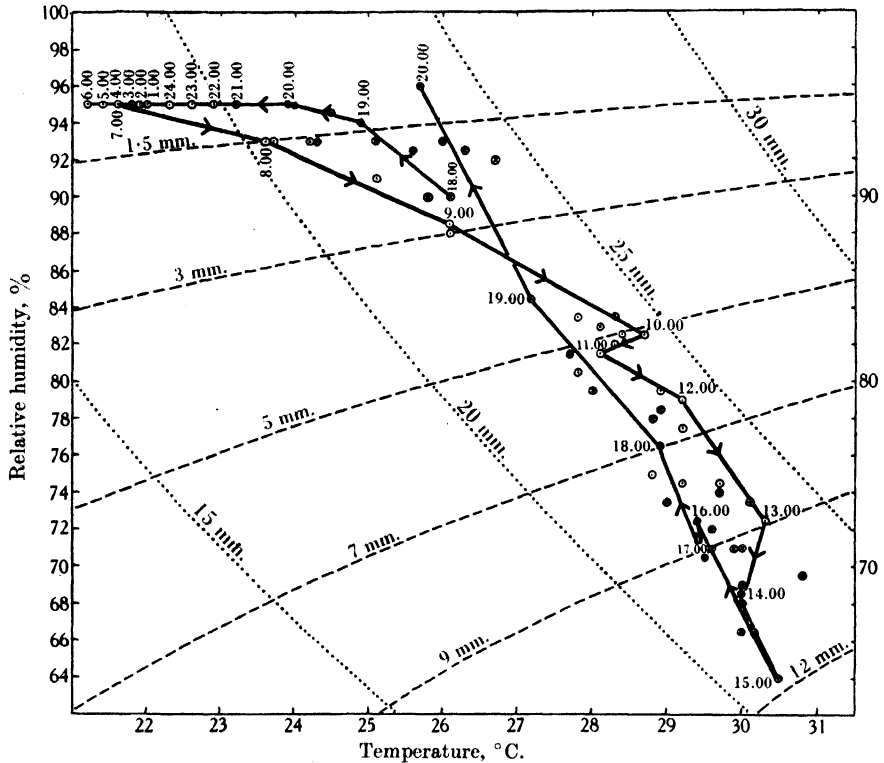


FIG. 6. Temperature and relative humidity at 23.8 m. in the canopy of primary forest in Nigeria, 10-11. v. 35.

during the evening, night, and early morning for the dry season in the undergrowth¹ (Fig. 3). The fall in vapour pressure from about 24 mm. at 10.00 to about 22 mm. at 14.00 is probably to be accounted for by the increased mixing with the outside air, both on account of convection due to sunflecks, and of the increased wind during the day. Fig. 4 shows that the outside air has a lower absolute humidity during the early part of this period. It is remarkable that a very similar relation is shown by the records in the tree tops, both in the dry

¹ It should be pointed out that although in both cases the fall in temperature during the period when the air was saturated with water vapour was about the same both inside and outside the forest, yet there was a copious dew outside the forest and none inside. It may be that the cooling of the lower layers takes place entirely by convection, thus leading to the deposition of all the dew on the top of the forest.

and wet seasons.¹ This continued high water content of the air must be due to the prevailing wind during the period of observation being from the sea, which is separated from the station by only 15 miles (24 km.) of low-lying country. As it is observed that the water vapour pressure in the tree tops falls during the morning, in spite of the water supplied by transpiration, it must be presumed that during the day we are dealing with mixing of the wetter layers in the tree tops with drier layers from above the trees.

The differences between the undergrowth and tree tops and the seasonal changes and their interrelations can be more fully understood if we consider them together in the same figure, and in the following two subsections we shall do this, separating the daily marches of temperature and humidity for convenience. The data used are those already considered, but the conclusions, although implicit in Figs. 3-6, are more clearly defined by this treatment of all four sets of observations together.

(b) *The daily march of temperature.*

Fig. 7 shows the march of temperature from 18.00 on one day to 20.00 on the next; the thicker pair of lines denote the canopy, and the thinner undergrowth, while the dry season is represented by solid lines and wet by broken ones. Each point gives the temperature at the time indicated; the quarter-hourly points have been omitted to avoid confusion. The curves for 8-9 March show clearly reversals of the temperature gradient between the canopy and undergrowth just before sunset and after sunrise, the temperature of the undergrowth remaining throughout the night about 0.4° C. above that in the canopy, which appears to fluctuate rather than fall between midnight and sunrise. On 10-11 May, on the other hand, the temperature gradient reversals take place about an hour or more later in each case. This is probably due to a lag in the cooling down and warming up of the canopy on account of the increased clouding in the wet season. There is a steadily falling temperature throughout the night in the canopy, while the undergrowth falls much less than on 8-9 March. This may be a general phenomenon, for as we have seen there is in the mean data of Tables II-V a much greater difference between the minimum temperatures in the canopy and undergrowth in the wet season than in the dry, though there seems to be no obvious reason why this should be so. The generally lower temperature in the wet season as compared with the dry is clearly shown, particularly in the undergrowth. The curves for wet and dry seasons only cross about 19.00 on the second day; on 9 March there was a

¹ There thus exists in the rain forest quite a different state of affairs from that observed by Buxton & Lewis (1934) in Northern Nigeria, to which we shall refer later. In the region near Gadau where they worked, the climate is much drier, the vegetation being principally thorn scrub, and closed forest is confined to the neighbourhood of water courses ("Fringing Forest"). In the open at Gadau in July, the beginning of the wet season, the absolute humidity rose from 16 mm. at 8.00 to 24 mm. at 18.00, and then fell steadily during the night. Records from the base of a tree in the "Fringing Forest" at the same period show a similar rise from 18 mm. at 8.00 to 26 mm. at 16.00.

storm, accompanied as always by a fall in temperature, which can be seen in the curve just after 18.00, and hence in the evening of that day the undergrowth temperature fell unusually low for the time of year.

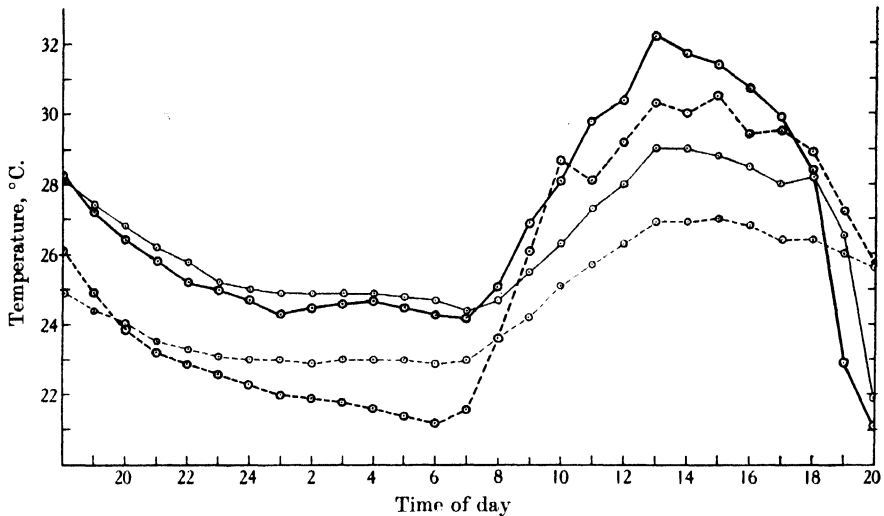


FIG. 7. The daily march of temperature in the undergrowth and tree tops of primary forest in Nigeria. (For explanation see text.)

(c) *The daily march of saturation deficit.*

In the absence of data on leaf temperature, the most important expression of the humidity when dealing with the transpiration of plants is the absolute saturation deficit. The daily march of this factor is plotted in Fig. 8 for the two situations and the two times of year already considered. This has been evaluated from the data for temperature and relative humidity given in Figs. 3-6, derived from quarter-hourly readings of the charts, a mean being taken for each hour. It will be noticed that the 24 hr. period in this case has been made to extend from midnight to midnight, instead of from 18.00 to 18.00; the latter period was used for convenience, as it coincided with sunset and the changing of the recorder charts, but it was thought that the former period would show the cycle of saturation deficit more clearly. It will be seen that with minor fluctuations the saturation deficit follows a regular course, rising steadily from 8.00 to about 14.00 and then falling to about 1 mm. at 20.00, at which level it remains throughout the night. We see again the effect of the storm on the evening of 9 March, the saturation deficit in the canopy having fallen sharply to a value below that in the undergrowth when the rain began.

The seasonal changes in saturation deficit in the undergrowth are considerable, there being 8 hr. on the day in March during which it exceeds the maximum during the day in May. Furthermore, neither of these months show extremes of low or high rainfall, which occur in December and July, so that the full seasonal range is not shown in the diagram. It is thus possible

that in the middle of the wet season the maximum saturation deficit might fall nearly as low as Stocker's figure of 0.5 mm. for Java (see below). On the other hand it is certainly much lower than the maximum of over 7 mm. recorded for the undergrowth of "Fringing Forest" in the drier climate of Northern Nigeria at the beginning of July, the early part of the wet season (Buxton & Lewis, 1934).

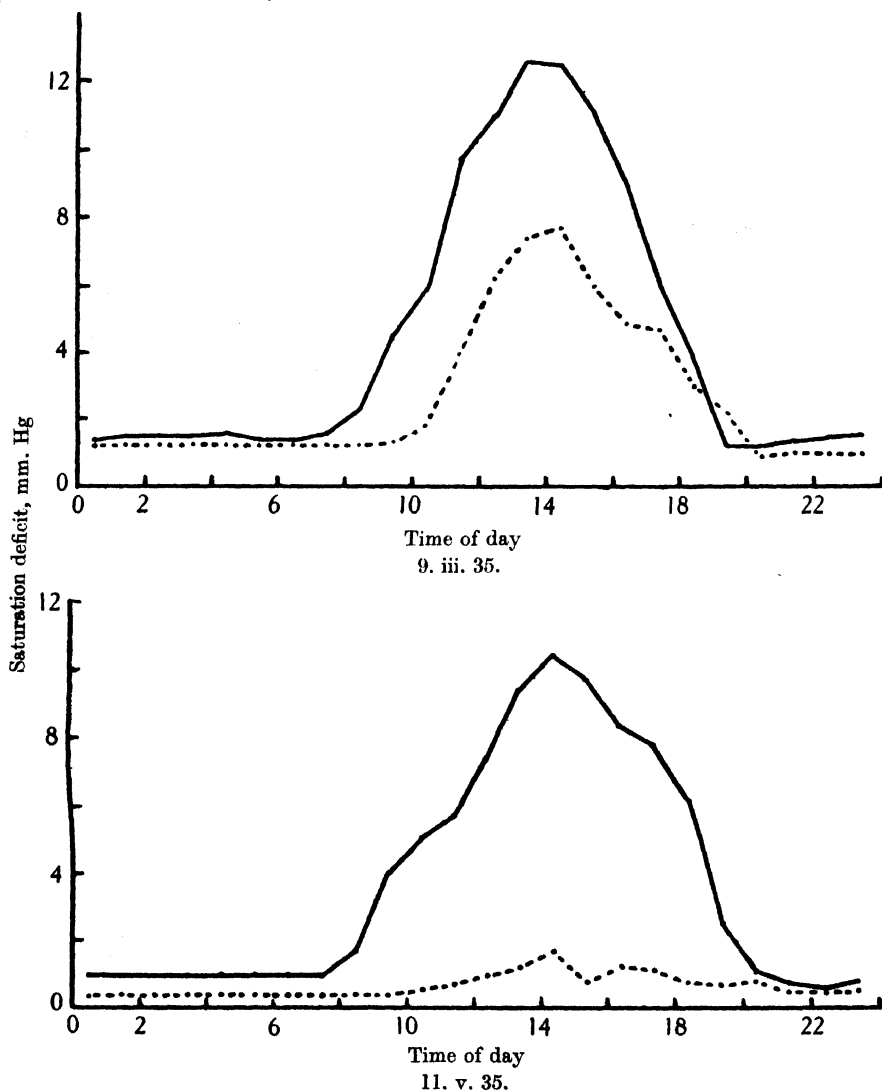


FIG. 8. The daily march of saturation deficit in primary forest near the Expedition's camp in the Shasha Forest Reserve.

Continuous lines—24 m. above ground in the canopy.

Dotted lines—0.7 m. above ground in the undergrowth.

Each point is a mean of four readings at quarter-hourly intervals.

(d) *Comparison with data for other tropical forests.*

Apart from the work of Buxton & Lewis (1934) already referred to, the writer is not acquainted with any published data for tropical forest to which the above method of analysis has been applied. There exist, however, sets of simultaneous observations of temperature and relative humidity, either in the form of figures or charts, in papers by McLean (1919) and Stocker (1935*a*, 1935*b*) and these can be compared with the data we have just considered. It should be mentioned that conditions in all the rain forest types examined by these authors differ in some respects from those in the Nigerian rain forest. McLean worked at Rio de Janeiro (23° S. latitude), where the temperature is on the average 4° C. or more below that in Nigeria. We have already remarked that the forest at Tjibodas in Java (Stocker, 1935*a*) is rain forest of a mountain type, situated at a height of 1300 m., and is colder, wetter, and much more open than the Nigerian type. General climatic conditions are more similar in Buitenzorg (Stocker, 1935*b*) where the temperature is comparable and the original vegetation was probably typical lowland rain forest; the chief difference is in the lower absolute humidity in the open air (circles in Fig. 11). Unfortunately the data for undergrowth cover only a period of four hours in the morning (crosses in Fig. 11), and so give us no information as to the daily march of temperature and humidity; as they do not relate to the same day as those for the open air, they merely give an indication that there may be a greater difference in absolute humidity between the undergrowth and the open air here than was observed by the writer in Nigeria.

McLean gives data for 10 and 11 December 1912 (that is to say, after the period of heaviest rainfall at the Jardim Botânico where he was working, the wettest months being July and October); as to locality and position he says (McLean, 1919, p. 24) "in the lowest stratum of the forest... in the shade of shrubs... the instruments being placed actually on the ground...". Fig. 9 gives readings from his charts for 10 December, and it is apparent that conditions in this forest are much drier than those in Nigeria. The duration of the maximum relative humidity on the two nights for which information is given was 7 and 2 hr., as against a mean of 14 for the dry season in Nigeria, while the saturation deficit at noon was 9.3 and 10.4 mm. Hg for the two days respectively, as against a maximum of 7.7 for the undergrowth on the day (9 March 1935) chosen as typical of the dry season in Nigeria. We notice, however, the same phenomenon as was observed in Nigeria, of large changes in saturation deficit accompanied by only small changes in absolute humidity, although in this instance the values of absolute humidity in the morning are higher than those in the afternoon, while in Nigeria there is a suggestion that the reverse is the case. As, however, the data presented in Fig. 9 represent the only complete 24 hr. period we have, it is not possible to say whether this difference is of general occurrence. As regards the influence of conditions

external to the forest on those in the undergrowth we have no information for Rio de Janeiro.

Stocker (1935*a*) made observations at Tjibodas in Java at three stations, A, 7 cm. above the forest floor, B, 1.7 m. above the forest floor in a fairly open

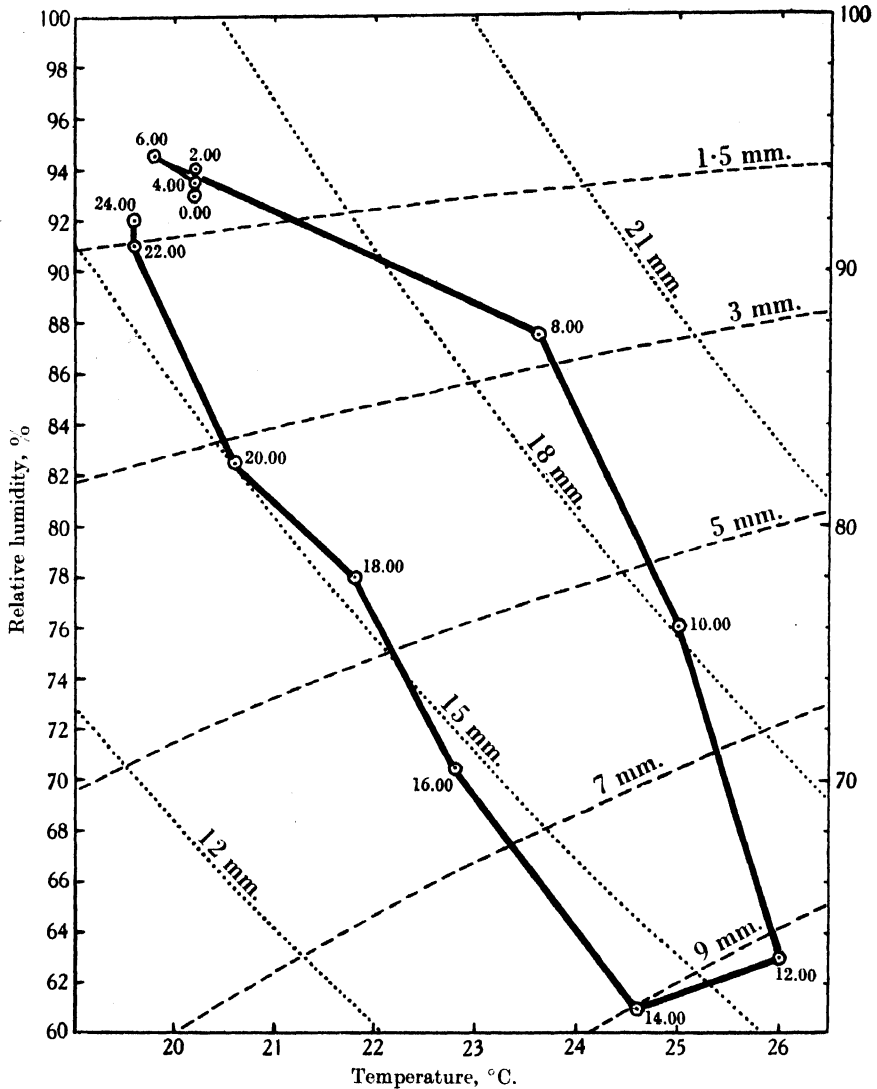


FIG. 9. McLean's observations at Rio de Janeiro, 10. xii. 12.

situation, and C, open ground in front of the Tjibodas guest-house, on three consecutive days (for a detailed description, see p. 445). At station A the relative humidity only once fell below 100% (to 99%) in thirteen observations, and these have accordingly not been plotted; all the data for stations B and C will be found in Fig. 10. The successive points for each separate day in station C

have been joined by straight lines to show the daily drift more clearly. It will be seen that the temperature is much lower, as would be expected from the altitude of 1300 m., and the undergrowth presents a picture similar to that of the wet season in Nigeria—partly as a result of the lower temperature the saturation deficit does not rise above 0.5 mm., as compared with 2.5 for

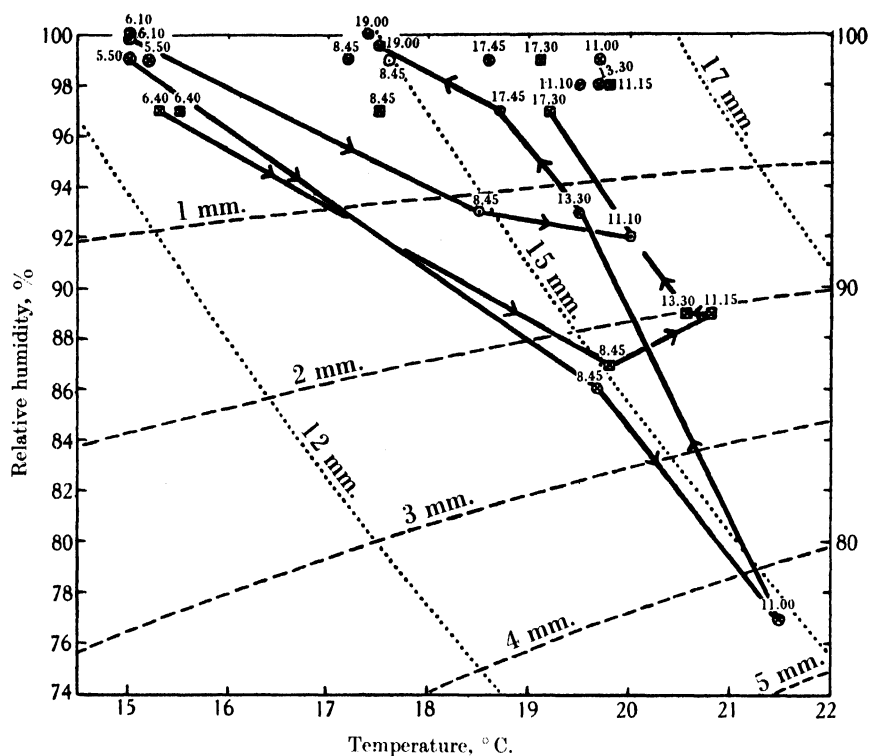


FIG. 10. Stocker's observations at Tjibodas in Java.

⊗ 7. iii. 30; ⊗ 8. iii. 30; ⊙ 9. iii. 30.

Nigeria in the wet season. The figures for the open ground, however, agree in form with the writer's, being clustered round the 15 mm. vapour pressure line. In this case, as in Nigeria, we notice that the vapour pressure is somewhat lower in the morning than in the evening, and also that in this case there must be a rapid fall in saturation deficit in the early afternoon, as the mean at 13.30 (1.6 mm.) is the same as that at 8.45.

We have already noted that there are very few data for undergrowth in the Botanic Gardens at Buitenzorg (Stocker, 1935*b*, Fig. 11), but there happen to be a set of thirteen observations on one day, at fairly regular intervals between 5.40 and 18.10, on temperature and humidity in a position which he describes as "at a height of 1.6-1.8 m. at the edge of the crown of the big *Cassia fistula* tree... that stands on the south side of the Treub Laboratory".

The meteorological measurements were made very close to the outer twigs of the tree, which faces East and South on to a small lawn. These observations are plotted in Fig. 11. They provide a very striking example of relative constancy of absolute humidity during large changes of temperature, resulting

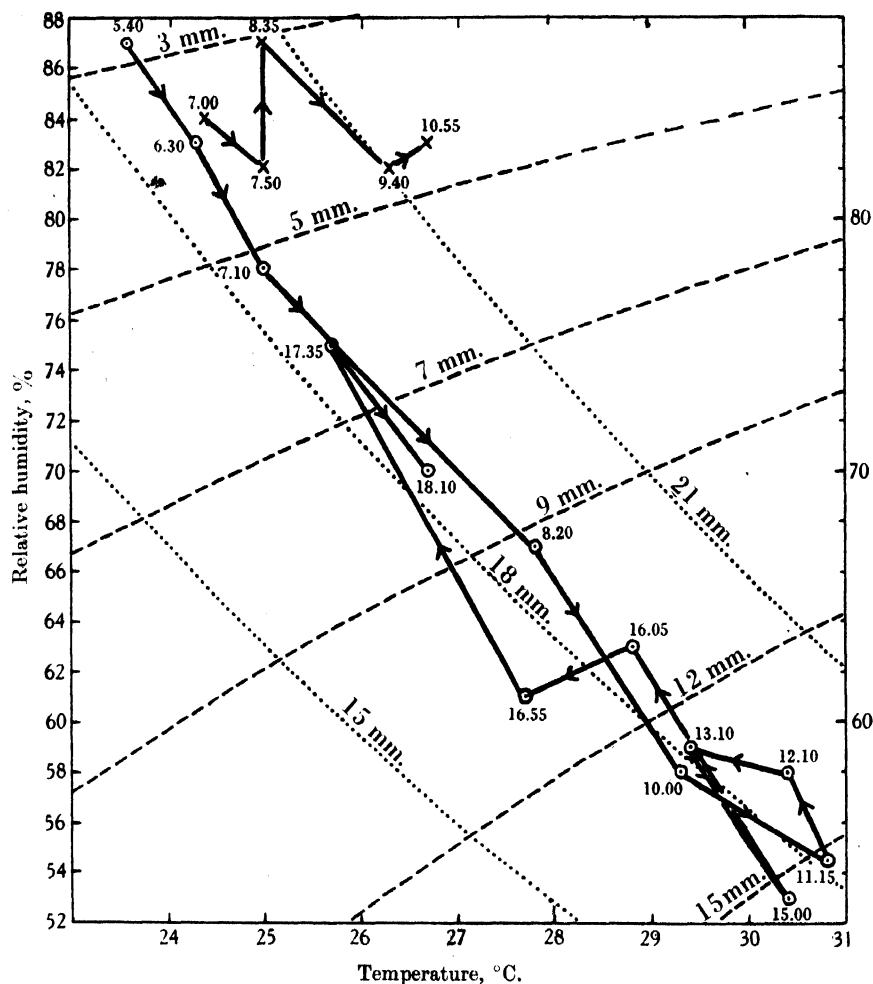


FIG. 11. Stocker's observations at Buitenzorg in Java.

○ 26. xi. 29, 1.6 m. open ground in garden;

× 29. xi. 29, 0.25 m. undergrowth in garden.

in large changes in saturation deficit, with a course very similar to that observed in Nigeria, and indicate that possibly this constancy of absolute humidity in the air near the canopy of a tropical rain forest may be a general phenomenon. Unfortunately, we are given data for only a single day, so that it is not possible to pursue the comparison further.

IV. INTENSITY OF ILLUMINATION IN THE UNDERGROWTH OF PRIMARY AND SECONDARY FOREST

The problem of the measurement of light intensity in tropical rain forest, or, indeed, in any other forest, is one of great complexity, and to provide any adequate description of the conditions of illumination the results of measurements of a large number of different types must be available. The following are the major complexities which must be taken into account.

When the sun is obscured by clouds, measurements of intensity of illumination at different stations in the undergrowth are sufficiently reproducible as to leave little doubt of the accuracy of any particular survey. It is a simple matter to measure both the range of intensities encountered in an area of forest at a particular time of day and the variations during the day in any one station. Variations caused by different degrees of clouding and by the annual rhythm in the intensity of sunlight (fortunately smaller near the equator than elsewhere) should also be determined.

When the sun is unobscured, however, the problem is much more complex. Whereas when there is no direct sunlight, changes in a particular station at a particular time, say, midday, may amount to two- or threefold, sunflecks may result in an increase in intensity of several hundredfold on the mean shade intensity. These sunflecks are, moreover, continually changing in position, size and intensity. The mean shade intensity in tropical rain forest is so low that such large increases in intensity possibly cause considerable increases in rate of photosynthesis (but see Discussion below), and they may thus be of the utmost importance in the life of a flora existing normally near the point where net photosynthesis during the day equals respiration during the night. An adequate study of sunflecks is thus essential in any picture of conditions of light intensity in forest. The increased intensity of the general shade illumination during sunshine as compared with clouded conditions should also be determined.

So far as the writer is aware, no such comprehensive information as that demanded by the above scheme has been obtained for any tropical rain forest. The data to be presented here do, however, give at least a partial picture of each of the main categories of information in this scheme. We shall make a detailed comparison of the shade intensity inside and outside a piece of secondary forest, and a comparison of the general conditions of illumination in this secondary forest with a number of stations in primary forest. Data on the incidence and intensity of sunflecks in these stations will be considered, and observations on illumination in a single station in primary forest at short intervals throughout a day. A major defect in all these data is that owing to the method of measurement it is not possible to express them in absolute units. A rough estimate of the intensity in metre candles can be made, but for light differing so radically in spectral composition from a standard candle as

this does, such a unit of measurement has little meaning. In particular, although some measurements were made using red filters, we have no satisfactory information on the intensity of illumination in the undergrowth in the spectral regions where most of the absorption by chlorophyll takes place.

(1) *Apparatus and methods*

The measurements were made with a Weston photoelectric cell, and suitable galvanometers; for measurements in the forest an Onwood galvanometer, with scale graduated from 0 to $12\mu\text{A.}$, was found sufficiently sensitive when readings were taken with colour filters. For higher currents a shunt, of a type designed by Atkins to shunt 1/1, 1/5, 1/20, and 1/100 without changing the resistance of galvanometer + shunt, was used, and by this means measurements were made in sunflecks and on occasion outside the wood. Normally for measurements outside a Ferranti $2\frac{1}{2}$ in. microammeter reading from 0 to $500\mu\text{A.}$ was used. A screen of flashed opal glass was placed over the cell during all readings, and the cell was supported facing vertically upwards, usually about 30 cm. above the ground. It was connected by a length of flexible cable about 3 m. long with the galvanometer, which was placed on a small table at which the observer sat. In the various series of observations described in subsections 2 (b) and (c) below readings were taken at 20 sec. intervals with a change of colour filter between each observation. A two-minute cycle was used, the six arrangements of colour filters being (1) opal glass only, (2) opal glass covering a 2 mm. plate of Schott's BG 12 (a blue glass), (3) opal glass only, (4) opal glass covering a 3 mm. plate of Corning's Sextant Green, (5) opal glass only, (6) opal glass covering a 2 mm. plate of Schott's RG 2 (a red glass).

The spectral sensitivity curve¹ of the Weston Type 1 photronic cell, and the effect on it of the various filters used are shown in Fig. 12, in percentage of the maximum sensitivity of the cell, which lies about 5800 Å. These curves, which are from data supplied by the makers in each case, apply to parallel light at normal incidence, and are thus not strictly applicable to our system, where the light is diffuse and the cell is covered by a plate of opal glass. They do, however, indicate the maximum range of wave-lengths over which the cell will respond when covered by any particular filter, and the maximum fraction of the incident light transmitted by each filter (as the transmission of the filter falls with increasing angle of incidence it must of course be less for diffuse light than for normally incident parallel light).

¹ Over a range of intensities including those recorded in the observations which follow, the current output of the cell under the conditions of the measurements is a close approximation to a linear function of the total intensity of incident daylight (see text, below). It may be presumed that this also holds for individual wave-lengths, although the writer has no information on this point. It is certain to be a close approximation to the truth for the very low intensities encountered in the undergrowth.

It must be borne in mind that the filter-changing cycle, as well as providing a series of comparable data, also involves a further source of error in the determinations—that introduced by the presence near to the cell of the person changing the filters. This error is likely to have a systematic, as well as a random, component, and cannot thus be estimated in its entirety by using statistics based on the mean of a number of ratios. The cell was usually placed about 20–30 cm. above the ground, and as the filter-changer lay down with

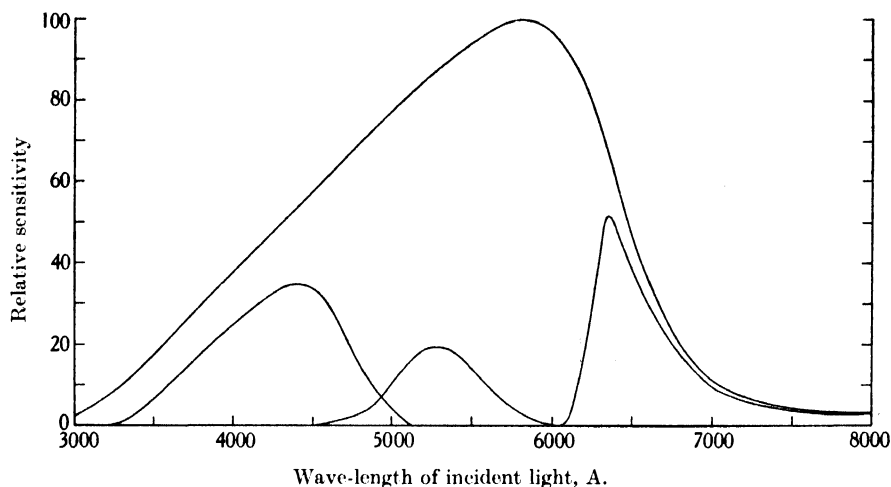


FIG. 12. The spectral sensitivity of the Weston photronic cell alone and in combination with various filters. For explanation see text, p. 466.

his hands below the level of the cell while readings were being taken, this error will not be very large, say from 1 to 10 %, though it is obviously impossible to measure it accurately.

An additional complication is introduced by the fact that the current produced by the cell is not a linear function of the incident light intensity; the departure only becomes considerable, however, for high intensities. It is quite negligible in all the readings taken in the forest shade; it might introduce an error of a few per cent into the readings in sunflecks (see below) but as these are only very approximate, it can be neglected here also. The largest currents which it was necessary to measure accurately were produced when readings were being made with the cell covered by coloured filters in the open, for comparison with simultaneous readings taken in the forest; with the red filter the current output might rise to $300\mu\text{A}$. A calibration of the cells and galvanometer kindly made by Dr W. R. G. Atkins before the writer left England indicated, however, that even with these maximum currents the error due to this cause did not exceed 1 or 2 %, and thus it too can be neglected in comparison with the random errors.

(2) Observations in Nigeria

(a) The variations of intensity of illumination in primary forest throughout the day.

Measurements were made on 4 March, at intervals of 10 sec. from 7.40 to 14.12 and of 15 sec. from 14.12 to 17.41. Intermissions totalled 17 min. during the 10 hr., and details of these will be found in Table VII (on pp. 470-1). A position was chosen in primary forest near the shelter containing recording instruments described on p. 448. The photocell was covered by a plate of opal

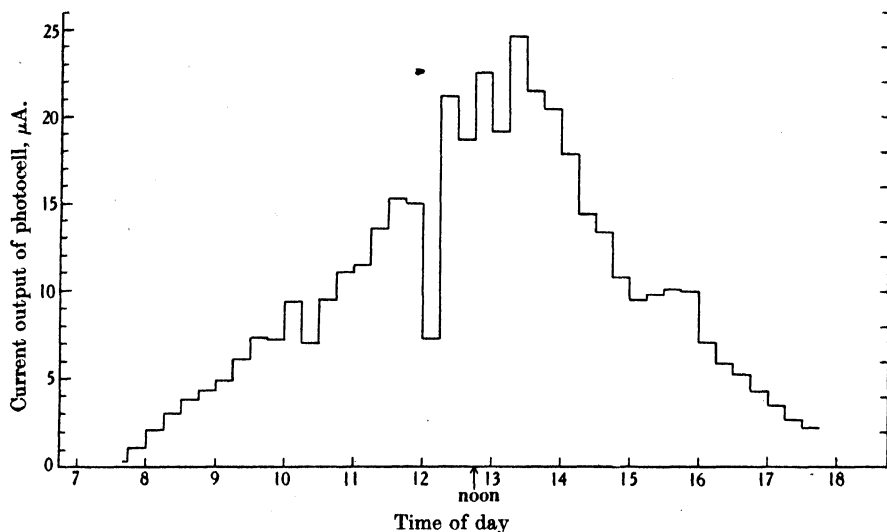


FIG. 13. The march of intensity of illumination in the undergrowth of primary forest in Nigeria, 4. iii. 35.

glass and supported, facing vertically upwards, at a height of 0.4 m. above the ground, near the lower leaves of a specimen of *Icacina trichantha* Oliv. (3142).¹ It may thus be assumed that the intensities of illumination in this spot were sufficient to support an undergrowth plant. Fig. 13 shows the march of intensity throughout the day, each line representing a mean of all the observations during a quarter of an hour (means of about ninety observations each before 14.15, and of about sixty after). The ordinates give the current output of the cell in microamperes. Over this range of intensities the output is proportional to the intensity, but only if the spectral composition remains unchanged. It will be seen that the change in intensity is very regular during the first and last 2 hr. of the observations, becoming more irregular in the middle of the day. The sun being higher in the sky, sunflecks appear, and the effect of clouding is greater. In spite of these factors, however, the changes in

¹ Numbers in brackets are the collecting numbers of Dr P. W. Richards (numbers over 3000) and of Mr R. Ross (numbers less than 300). A set of specimens is deposited in the British Museum. Native names are also given when available.

intensity are fairly regular, and this is confirmed by a closer examination of the individual readings. Only for a total of 31 min. out of the 10 hr. does the intensity rise more than 20 % above the mean value for the quarter-hour concerned, only for 3.4 min. more than 100 % above, and only for 0.5 min. more than 400 % above (see Table VII). The maximum shade intensity corresponding to about $25\mu\text{A.}$ is of the order of $\frac{1}{2}$ –1 % of full sunlight at the same time (see below), so we see that the sunflecks are both infrequent and of low intensity compared with the external illumination. Furthermore, if we take sunflecks as corresponding to the level of more than 100 % above the mean intensity, we see that they are confined to a period of about 4 or 5 hr. in the middle of the day. At other times sunflecks are absent owing to the decreasing transparency of the canopy with decreasing altitude of the sun. This observation on the incidence of sunflecks based on duration is of the same order as the estimates based on area given by Carter (1934) for rain forests in British Guiana, the percentage of the observed area occupied by sunflecks being in most cases of the order of 1 %. We shall consider further evidence on the duration of sunflecks below.

(b) *A comparison of primary with 14-year-old secondary forest.*

In addition to the data detailed in the previous paragraph, observations were made in a number of stations in primary forest, usually at a height of about 0.3 m., near plants of *Icacina trichantha* Oliv. (stations I, II, III) or *Rinorea* sp. (3171 etc.) (stations IV, V), typical components of the "herb layer". As in the previous observations the cell was covered by a plate of opal glass, and faced vertically upwards. Observations of the current output were made at intervals of 40 sec. during the period indicated in Table VII, and notes were made of whether there were any visible sunflecks on the cell at the time of observation, and also of the degree of clouding (see the next subsection for details). In Table VII are set out the maximum and minimum currents during each period of observation, the duration of visible sunflecks, and of periods when the output exceeded twice and five times the mean value when the sun was unobscured. It will be seen that on the average these durations of intensities of illumination higher than the normal form only a small fraction of the total. The table also records the maximum current recorded which was not counted in these periods of higher intensity, this value and the minimum thus defining the observed limits of variation of the shade light. It will be seen that the station considered in the previous subsection corresponds roughly in range of normal shade intensity with the lightest of these five stations, although the mean incidence of bright sunflecks (more than five times the shade intensity) in these latter stations is higher, covering about $2\frac{3}{4}$ % of the total time of observation; as would be expected, however, the variability is high. We may conclude that the station previously considered gives a picture which is typical of the diurnal changes of intensity in the forest.

Table VII. *Illumination in the undergrowth of forest in the Shasha Forest Reserve, Southern Nigeria. Cell surface 0.3 m. above the ground unless otherwise stated*

Situation	(1) Date and time		(2)	(3)
			Min. reading $\mu\text{A.}$	Max. reading excluding values in columns 6-8 $\mu\text{A.}$
Primary forest near Odoko tree, height of all 0.4 m.	4. iii	7.41-11.00	0.2	15.5
		11.00-12.00	7.4	24.1
		12.00-13.00	4.2	40
		13.00-14.00	12.1	39
		14.00-15.00	9.3	23.3
		15.00-16.00	5.9	12.9
		16.00-17.40	1.9	8.3
Primary forest				
Station I, sample plot 1 of Richards (1939)	12. iv.	12.06-12.32	20.0	26.4
Station II, sample plot 2 of Richards (1939)	16. iv.	11.41-12.17	7.9	27.9
Station III, another part of sample plot 2	16. iv.	12.51-13.30	16.3	43.1
	22. iv.	10.50-11.22	12.8	33.9
	9. v.	10.00-10.36	3.7	31.1
Station IV, near sample plot 2	22. iv.	12.40-13.06	7.9	17.1
	9. v.	11.54-12.48	6.0	12.1
	24. v.	11.40-12.42	1.6	12.2
Station V, about 5 m. from station IV	22. iv.	12.01-12.38	5.2	11.2
	9. v.	11.00-11.52	5.1	12.5
	24. v.	11.16-11.38	4.0	10.0
Secondary forest: sample plot II of Ross (forthcoming contribution to these "Studies")				
Station 2	17. iv.	12.23-12.55	48.0	73.0
	23. iv.	12.10-12.42	28.0	73.4
	21. v.	13.12-14.14	31.9	77.8
Station 1	17. iv.	11.30-11.54	13.2	20.0
	23. iv.	11.30-12.00	10.3	18.5
	21. v.	11.54-13.00	5.6	16.3
Station 4	17. iv.	13.44-14.18	9.0	17.2
	23. iv.	13.30-14.02	4.2	14.8
	23. v.	13.00-14.02	4.5	15.0
Station 3	17. iv.	13.04-13.36	10.7	15.6
	23. iv.	12.50-13.22	6.2	14.1
	23. v.	11.50-12.52	3.8	11.8

Table VII (*cont.*)

(4) Max. reading μ A.	(5) Duration of deter- minations min.	(6) Duration of visible sun- flecks on the cell surface min.	(7) Duration of readings > twice the mean shade reading with the sun unclouded min.	(8) Duration of readings > 5 times the mean shade read- ing with the sun unclouded min.	Weather
15.5	196.5	—	0	0	Overcast and a few drops of rain about 8.30. Later fine and sunny with some cloud
24.1	59	—	0	0	
43	57.5	—	0.3	0	
122	57	—	2.8	0.5	
23.3	57	—	0	0	
26	58	—	0.3	0	
8.3	98	—	0	0	Cloudy
	583	—	3.4	0.5	
26.4	26	0	0	0	
252	36	—	10.7	6.0	
209	39	—	3.3	2.0	
33.9	32	1.7	0	0	
44.0	34	1.5	1.0	0	Sunshine for 20 min. Sunshine for 27 min. Sunshine for 5 min.
	105	3.2	4.3	2.0	
17.1	26	0	0	0	
14.8	54	2.5	0	0	
20.5	62	1.0	0	0	
	142	3.5	0	0	Sunshine for 23 min. Sunshine for 48 min. Sunshine for 3 min.
244	32	13.7	8.0	2.7	
13.8	52	4.7	0	0	
10.0	22	0	0	0	
	106	18.3	8.0	2.7	
	389	25	23	10.7	Sunshine for 25 min. Sunshine for 35 min. Cloudy
73.0	32	—	0	0	
131	32	0	1.3	0	
353	58	7.0	4.7	2.7	
	122	7.0	6.0	2.7	
20.0	24	—	0	0	Sunshine for 10 min. Sunshine for 28 min.
18.5	30	0	0	0	
22	66	2.3	0.3	0	
	120	2.3	0.3	0	
17.2	34	—	0	0	
14.8	32	0	0	0	Sunshine for 25 min. Sunshine for 31 min.
18.2	62	1.5	4.0	0	
	128	1.5	4.0	0	
15.6	32	—	0	0	
14.1	30	0	0	0	
13.8	62	3.8	0.3	0	Sunshine for 16 min. Sunshine for 42 min.
	124	3.8	0.3	0	
	494	14.7	10.6	2.7	

Similar data were obtained for four stations in 14-year-old secondary forest on Mr Ross's sample plot II (to be described in a forthcoming contribution to these "Studies"). A description of these stations is given in the next subsection. The same plan of observation as that used in the primary forest stations was adopted, and the data for these four stations are also set out in Table VII. It will be seen that the three darkest stations are comparable with the four darkest primary forest stations, but that the lightest station is considerably lighter than the lightest station in primary forest, as is also indicated by the luxuriance of the undergrowth (see description of station 2 below). On the whole it appears that the incidence of periods of high intensity is lower than in the primary forest. If this difference is real it may be due to the level and continuous, though not dense, canopy of *Musanga Smithii* R.Br. at about 23 m.

It thus seems likely that a similar range of intensities of illumination is to be found both in primary and in 14-year-old secondary forest. Before we can reach a definite conclusion, however, we must have information on the spectral composition of the light in these two types of forest, as owing to the selective sensitivity of the cell it is quite possible to obtain the same current in two situations without the intensity in these two places being identical either to the eye, in absolute units, or in photosynthetic value for any particular system. Information on this point is provided in Table VIII. In it are set out ratios of the current recorded when the cell was covered by a filter and a plate of opal glass to the current recorded when the cell was covered by the opal

Table VIII. *Spectral composition of the illumination in undergrowth in the Shasha Forest Reserve. Mean ratios as percentages, with fiducial values. For explanation see text. Numbers in brackets below a mean indicate the number of ratios on which it is based*

	Bright sunlight			Sun completely obscured		
	Blue filter	Green filter	Red filter	Blue filter	Green filter	Red filter
Primary forest						
Station III	7.05 ± 0.49 (9)	5.94 ± 0.18 (7)	30.0 ± 1.5 (10)	9.02 ± 0.27 (6)	6.16 ± 0.17 (7)	20.1 ± 1.4 (7)
Station IV	5.70 ± 0.14 (8)	5.40 ± 0.06 (5)	34.1 ± 0.7 (6)	8.16 ± 0.23 (14)	6.10 ± 0.18 (14)	25.8 ± 1.5 (18)
Station V	5.17 ± 0.39 (27)	5.46 ± 0.11 (24)	36.5 ± 1.8 (29)	7.84 ± 0.20 (13)	6.01 ± 0.15 (16)	26.9 ± 0.6 (13)
Secondary forest						
Station 2	7.16 ± 0.20 (3)	6.12 ± 0.14 (4)	26.8 ± 1.4 (5)	8.51 ± 0.23 (13)	6.26 ± 0.18 (11)	21.2 ± 0.7 (12)
Station 1	5.66 ± 0.49 (9)	5.43 ± 0.29 (6)	35.2 ± 1.9 (6)	7.46 ± 0.24 (10)	5.56 ± 0.28 (9)	27.8 ± 0.6 (11)
Station 4	5.06 ± 0.17 (14)	4.98 ± 0.12 (16)	39.8 ± 0.7 (17)	7.63 ± 0.49 (7)	5.62 ± 0.18 (9)	26.9 ± 1.1 (10)
Station 3	4.94 ± 0.18 (22)	4.96 ± 0.14 (19)	39.4 ± 1.7 (20)	7.40 ± 0.78 (6)	—	27.2 ± 3.7 (4)

glass alone. This latter value was obtained by taking a mean of readings 20 sec. before and 20 sec. after the reading with the coloured filter; ratios for periods when rapid changes in intensity were taking place were rejected. Mean ratios and their fiducial values¹ are given for the four situations in secondary forest, and for three of the primary forest stations, in each case for red, green, and blue filters (see Fig. 12 for details of the transmission of these filters); and again in each case for two conditions, the sun completely unclouded and completely obscured. The ratios comprise only readings when there was no visible sunfleck on the cell. As would be expected the degree of clouding of the sun has a considerable effect on the composition of the light on the forest floor. It will be seen that there are no marked divergences in composition between primary and secondary forest as measured by these filters, and though these ratios do not give us any absolute information as to the composition of the light on the forest floor (as witness the ratios for "red" light to which we shall return later) owing to the wide range of wave-lengths covered by each of them, yet seeing that the ratios refer to forests similar in structure, receiving a similar external illumination, we may conclude that the composition of the light in the two is essentially the same.

It is interesting to make a rough estimate on a basis of these ratios of the spectral distribution of intensity in the darker parts of the forest. Let us take as an example station 4 in the secondary forest with the sun unobscured. The ratio of the reading with the blue filter to the reading without is 5.06 %, and since in the region of maximum transmission of this filter (between 4050 and 4350 Å.) it transmits 66.4 % of the incident light (at normal incidence), we can say with confidence that at least 5.06 divided by 0.664, or 7.6 % of the total diffuse illumination inside the forest must fall within the limits of transmission of the blue filter (3200–5000 Å.). Similarly for the green (maximum transmission 22.2 % between 5200 and 5300 Å.) and the red (maximum transmission 87.8 % beyond 7000 Å.) filters we can say that at least 22.4 % of the total diffuse illumination falls within the limits 4700–5900 Å., and 45.3 % beyond 6000 Å., respectively. We have thus accounted for 75.3 % of the total, the remaining 24.7 % being due to these figures being calculated on maximum transmissions. It will be divided between these regions in some way impossible to estimate. However, it is obvious that when some of this remainder has been deducted for the blue and green regions so little remains in relation to the large minimum percentage for the red region that most of this, *c.* 40 % of the total recorded, illumination must lie in the region of maximum transmission of the red filter, above 7000 Å., indicating a considerable increase in the transmission of the canopy of the forest just beyond the visible spectrum, of which we shall also find evidence from a different line of approach below. Data showing a similar phenomenon in temperate woodlands have been given by Atkins & Poole (1931) and Seybold (1936).

¹ See footnote on p. 440, and note on Table IX.

(c) *A comparison of the intensity of illumination inside and outside 14-year-old secondary forest.*

When comparing the external and internal intensities of illumination, it is obviously necessary that the places of measurement should be close together. In the case of primary forest, this would only be possible if a station were established above the forest, as on account of the method of administration of the Forest Reserve no clearings of sufficient extent existed in primary forest. Measurements were however made on a plot of 14-year-old secondary forest (this will be described by Mr R. Ross in a later contribution to these "Studies" (sample plot II)) in four situations representative of conditions in the undergrowth there. Mr Ross kindly assisted in making these measurements and the descriptions of the secondary forest which follow are from his observations.

After 14 years the regenerating vegetation had reached a height of about 75 ft. (23 m.), where there was an almost closed, but nevertheless thin canopy of *Musanga Smithii* R.Br. At about 15 ft. (5 m.) from the ground there was a complete canopy, closed over almost all the area considered, principally of the shrubs *Conopharyngia penduliflora* (Stapf) Stapf (9 etc., Idapopo) and *Rinorea* sp. (Epinpairoko). Between these two layers were a number of trees of varying height forming no regular layer. The ground flora was very sparse except in the occasional openings in the shrub canopy, in one of which (station 2) observations were made. The average of ten counts of the number of plants of all kinds on a quadrat of 9 sq. m. on this plot was about 50, as against 250 in primary forest, this difference consisting mostly of tree and shrub seedlings below the height of 30 cm., and to a lesser degree of herbs. At this stage the undergrowth is thus less dense than that in primary forest as far as herbs go, and the small, slow-growing, spindly shrubs so characteristic of the primary forest are not yet established in such quantity. It is probably owing to the very dense shrub canopy at a height of about 5 m. in addition to the tall trees that the floor of the forest appears to the eye to be on the whole darker than the primary forest, as was indicated by the figures in Table VII. As far as it is possible to judge by eye alone it seemed that at 14 years old the secondary forest had passed its maximum density, and the light intensity near the ground had increased.

The measurements of the external intensity were made in a large clearing, with the cell at a height of about 25 cm. above the ground, the low table at which the observations were recorded being about 3 m. away. This spot was about 100–200 m. from the interior stations, of which there were four, and the following is a description of the forest in the neighbourhood of these.

Station 1. There is a thick canopy of *Rinorea* sp. (Epinpairoko) at a height of 4 m. with an opening above to the crowns of *Musanga Smithii* R.Br. at 23 m. About 3 m. away from the station is a specimen of *Discoglypsemna caloneura* (Pax) Prain (3221, etc., Jesebe) about 12 m. high. On the ground are occasional specimens of *Cyanastrum cordifolium* Oliv. (3083, etc.).

Station 2. This is situated in an opening about 5 m. in diameter which reaches to the canopy of *Musanga Smithii* R.Br. at about 23 m. The cell was placed close to the edge about 1.5 m. from the base of a *Canthium glabriflorum* (K. Schum.) Hiern (129, etc., Ajelera), about 10 m. high, and 1.5 m. from the base of two specimens of *Rinorea* sp. (Epinpairoko). On the other side of the clearing about 3 m. from the cell are two specimens of *Lophira procera* A. Chev. about 6 m. high. The ground flora consists of *Pteris Preussii* Hieron. (51) and *Piper guineense* Schum. (3041).

Station 3. The station is surrounded at a distance of about 3 m. by three specimens of *Musanga Smithii* R.Br. about 23 m. high and one *Fagara macrophylla* (Oliv.) Engl. (3433) about 15 m. high, while a little closer, at a distance of 2 m., are the stems of two small saplings of *Sarcocephalus Diderrichii* De Wild., and a specimen of *Conopharyngia penduliflora* (Stapf) Stapf (9, etc., Idapopo) about 4 m. high. There is a closed canopy of *Conopharyngia penduliflora* and *Rinorea* sp. (Epinpairoko) at about 4 m. in the whole of this neighbourhood. The ground flora consists of abundant seedlings of *Diospyros chrysantha* Gürke (72, Ogwagwa) from 0.6 to 1.2 m. high.

Station 4. There is a canopy of *Musanga Smithii* R.Br. at about 23 m., the nearest one being 6 m. away. Below this is a canopy at about 6 m. composed of *Conopharyngia penduliflora*, *Rinorea* sp. (Epinpairoko), *Rinorea* sp. (242, etc., Ombe) and others. There are also a few specimens of *Conopharyngia penduliflora* and *Rinorea* sp. below 2.5 m. in height.

At all these interior stations the arrangements of cell and observer were similar to those outside, and they are described in detail on p. 474. Unfortunately the intensity of full sunlight in the tropics is so high that heating of the exterior cell is considerable, resulting in a drop in sensitivity when the cell is exposed to full sun. Accordingly the expedient recommended by Atkins & Poole (1926) was adopted and the cell was screened from the sun by a small disk placed about 2 m. away. Readings in the presence of sunflecks within the wood were rejected and attention paid only to shade light.¹ Under these conditions it was found that the major source of variation in the ratios of internal to external intensity (for which Atkins & Poole (1926) proposed the term "daylight factor") was the degree of clouding of the sun's disk, and this was noted against each reading. Table IX gives data only for the cases when the sun was either quite unobscured or completely obscured—no trace of sunflecks being visible in the wood. This table sets out means of ratios of internal to external diffuse light intensity at the same time for the four stations, the three

¹ Comparisons of readings inside and outside the forest are of course only justified when the sun is obscured by cloud (i.e. for perhaps half the day). The ratios when there is bright sunshine are only useful in arranging the situations in order of intensity of illumination in the undergrowth. It is a pity that when making these measurements the writer did not think of using a large neutral filter, such as a perforated plate, which could have been held some distance away, thus avoiding heating of the photocell and at the same time allowing total illumination outside the forest to be measured, an arrangement which has been used in subsequent work in England.

Table IX. *Mean ratios of intensity of vertical illumination inside to outside 14-year-old secondary forest, as percentages*

	Bright sunlight			Sun completely obscured		
	Blue filter	Green filter	Red filter	Blue filter	Green filter	Red filter
Station 2	2.43 ± 0.72 (4)	3.57 ± 1.83 (3)	6.44 ± 2.03 (3)	2.05 ± 0.27 (12)	2.30 ± 0.10 (12)	3.41 ± 0.16 (11)
Station 1	0.60 ± 0.09 (9)	1.06 ± 0.12 (6)	2.74 ± 0.44 (9)	0.37 ± 0.04 (7)	0.48 ± 0.06 (7)	1.04 ± 0.10 (7)
Station 4	0.40 ± 0.04 (13)	0.65 ± 0.04 (13)	2.37 ± 0.13 (15)	0.36 ± 0.05 (6)	0.41 ± 0.04 (7)	0.88 ± 0.07 (10)
Station 3	0.28 ± 0.025 (20)	0.47 ± 0.04 (21)	1.67 ± 0.12 (21)	0.30 ± 0.11 (3)	—	0.65 ± 0.15 (3)

The characteristics of the filters used are described on p. 467.

The number of separate ratios on which each mean is based is placed beneath in brackets; the means are followed by the appropriate fiducial values (see footnote on p. 440). When two means differ by more than the sum of their respective fiducial values there is usually a high probability that they are really different; e.g. with the red filter and the sun obscured the difference between the means for stations 1 and 4 is 0.16 %, and although the sum of their fiducial values is 0.17 the probability of the two being really different is considerably more than 100 to 1.

different colour filters, and the two conditions of the sun. The fiducial value of the mean is given in each case, and also the number of observations on which it is based. Details of the days and times at which observations were made at the various stations have been given in Table VII. The observations were restricted to within an hour or so of noon, and in each station we have taken a mean of observations made on two days separated by a month (23 April and 21 or 23 May). The following remarks apply only to the data for the periods when the sun was obscured.

There is obviously no difficulty in arranging the four stations in order of decreasing ratio of internal to external illumination, which, seeing that the stations are close together, also means order of absolute intensity of illumination; all three spectral regions give the same result. The range of variation in the three darkest stations is not great, and as we have seen above we may assume a similar range of ratio in the case of primary forest—probably on the whole one somewhat higher.

The ratios obtained with the red filter are in all cases much larger than either the green or the blue. This is almost certainly due to a region of high transmission by the leaves at wave-lengths just beyond the visible (see above), where the cell is still sensitive and when chlorophyll absorbs little (the cell alone retains about 11 % of its maximal sensitivity at 7000 Å., where the normal eye has only 1 %, and it still retains 3–4 % at 8000 Å.). The observations of Carter (1934) do not conflict with this hypothesis; his ratios usually show somewhat lower values for the red than for the green and blue, but his cell retained very little sensitivity at 7000 Å., and had none beyond about 7300 Å. The ratios with the red filter in position given in Table IX thus give

us only a minimal value for the decrease in intensity in the region of the absorption of the chlorophyll absorption bands in the red.

With these limitations it will be seen that this table gives us a picture of the relation between internal and external illumination as far as the diffuse light in each situation is concerned,¹ and thus a true picture for that part of the day when the sun is obscured by cloud (probably on the average about half); unfortunately no extensive data on this point were obtained. Table VII gives some information for the periods when degree of clouding was being observed, but these periods were only very short.

Thus when the sun is obscured it seems likely that the ratio of internal to external intensity throughout most of the visible spectrum is between a third and a half per cent; it is likely to be lower in the regions where chlorophyll absorbs most, so that the above is an upper limit for the effective radiation, and in the near infra-red it rises rapidly to a value at least two or three times as large.

When the sun is unobscured, we have not only eliminated from our measurements of exterior intensity more than half the total intensity by shading off the sun, but also eliminated a source very different in spectral composition from diffuse light, the maximum intensity being shifted towards the red end of the spectrum. Inside the forest, however, there is no similar shading, only the sunflecks resulting from the direct penetration of sunlight into the forest being rejected. We should thus expect an increase in the ratios as compared with clouded conditions, an increase which should be greater for the red than for the green and for the green than for the blue filters, and this is what Table IX shows. Of course it is possible that the true ratio of internal to total external illumination may have fallen, but although we have no information on this point it seems likely that if there is such a fall it is not very great. The chief interest in this section of the table lies in the fact that the order of absolute intensity which we have already found for clouded conditions at the four stations is unchanged in bright sunlight if sunflecks are excluded.

(3) *Comparison with observations in other tropical rain forests*

Extensive observations on light intensity in rain forests have been published by Allee (1926) and Carter (1934) for Panama and British Guiana respectively, and also by Moreau (1935) for forest at 1150 and 3000 ft. (350 and 900 m.) in the Usambara mountains, East Africa. This latter is less comparable with the Nigerian rain forest than the two former. Although

¹ The sensitivity of the cell and filter system we have described is a function of the angle of incidence of the light. As it is almost certain that the distribution of intensity over a hemisphere is different inside and outside the forest, this introduces a systematic error, of a magnitude which it is not possible to estimate accurately, into all these ratios. It is likely that this will be positive, and in the worst possible case it should not exceed 50 %. The true ratios should thus all be smaller than those given, lying between the value given and one two-thirds as large, but likely to be nearer the value given.

Allee's observations cover a large number of habitats and a large range of intensities, he gives no information on the duration of particular intensities or on the relative area occupied by the sunflecks whose intensity is recorded, and the readings given show so great a variability that it is not possible to obtain much information from them on the illumination in any particular community over a period of time. Carter's ratios of intensity inside to total intensity outside for various types of rain forest in British Guiana are, however, comparable with the observations in section (c) above. (Measurements were made consecutively outside and inside the forest, the cell being exposed for only a very short time outside to avoid heating as far as possible.) Not counting sunflecks, four out of five stations in different forest types give ratios varying from 0.28 to 0.35 % for a red filter, from 0.30 to 0.41 for a green and from 0.28 to 0.41 for a blue, the figures for the fifth station being 0.16, 0.18 and 0.18 respectively. The difference in the ratios with red filters between these observations and those of the writer we have already considered, and it will be seen that in the case of the green and the blue filters, where the two sets of apparatus are more nearly comparable, the observations in British Guiana and in Nigeria appear to give results of the same order. We have also already seen that Carter's estimate of the area occupied by sunflecks in the British Guiana forests is similar to the observations of the writer in Nigeria.

For the Usambara mountains Moreau gives observations of the light intensity in the forest shade about noon on bright days. Excluding sunflecks, on which he gives no data as to area or duration, both types of forest, the mountain and lowland types, agree in giving ratios of internal to external intensity of about 0.1 %, which it will be seen is less than either the writer's observations or those of Carter. The observations were, however, made using a visual comparison photometer, and the differences in spectral composition between the standard and the light inside the forest may have introduced complications. No readings with colour filters being available, it is not possible to say whether this was so or not.

V. DISCUSSION: THE RELATION OF THE ATMOSPHERIC ENVIRONMENTAL CONDITIONS TO THE LIFE OF THE PLANT

We have seen that in the undergrowth there exist conditions of equable temperature and low saturation deficit. Extremes of temperature and lack of water are thus not likely to be of importance in limiting the activities of the undergrowth flora. These activities may of course be controlled by environmental factors other than those which we measured, e.g. there might be a lack of mineral nutrients in the soil, but in this forest the dark green foliage so characteristic of the undergrowth does not suggest lack of essential salts. It is also worth mentioning that plant diseases appear to be very uncommon in tropical rain forest, signs of fungal attack on living plants being very seldom seen. It seems likely, therefore, that the very slow rate of growth of plants

on the forest floor is due to a low rate of photosynthesis, leading to a lower rate of net increase over a 24-hour period, some of the gain during the day being respired during the night. Obviously under these circumstances any factor which causes a small increase in assimilation rate may be of great importance in the life of the plant.

The rate of photosynthesis will be a function of the intensity of illumination ("light limiting"), or of the carbon dioxide concentration ("carbon dioxide limiting") or of both if we are dealing with the intermediate region of interaction of the two factors in the photosynthetic process. However, if carbon dioxide is limiting the rate of photosynthesis, light intensity may yet have an important effect via stomatal aperture. We have no information in the case of these plants of tropical rain forest undergrowth to enable us to decide which of these is in fact realized, but it may nevertheless be useful to consider the various possibilities. We have seen that the carbon dioxide concentration during the part of the day investigated is considerably above "normal", though it is highest in the early morning up to 10.00 when the intensity of illumination is on the whole less than a third of that about midday. If carbon dioxide concentration is limiting (and if the stomatal resistance is high this may be the case down to very low light intensities) then this increased carbon dioxide concentration will be an important factor, though hardly in the sense of the conception of a "carbon dioxide flora". It has been shown that the daily march of intensity of illumination in the undergrowth follows a fairly steady course, with few major deviations, remaining for most of the time below 1 % of the external intensity, but rising for short periods (of the order of 1 % of the total time of daylight) to values more than twice as high, and for still shorter periods to more than five times the steady shade value. If light intensity is limiting, then these periods, short as they are, will be important in increasing the assimilation rate, but if the rate of the photosynthetic process itself is limited by the carbon dioxide concentration, as would certainly be the case if the stomata were almost closed, these periods of higher light intensity might be of importance in causing stomatal opening (which might very well persist for some time as an "after effect") and thus reducing the resistance to the entry of carbon dioxide into the leaf.

Carbon dioxide at these concentrations is not likely to have effects on the life of the plant other than via the rate of photosynthesis, but light intensity, on the other hand, may affect other aspects such as the rate of cell division or elongation. Again we have no information on the reactions of this type of plant to the naturally occurring range of these conditions.

It may be interesting here to mention one or two observations on the distribution of the two undergrowth species in which the writer was especially interested, *Icacina trichantha* Oliv. and *Rinorea* sp. (3171). The distribution of these two plants differed widely, for whereas *Rinorea* sp. was confined to the forest shade, *Icacina trichantha* grew there and also outside the forest, even

completely exposed on dry hillsides. Experiments were made on these two species in potometers, and it was found that both would stay alive for several days in a potometer in the forest undergrowth without experiencing any large permanent water deficit (excess of loss of water over uptake). However, whereas an *Ipomoea trichantha* shoot from the deepest shade would withstand being brought into the much warmer air of the laboratory, where the transpiration rate was four to five times as high, without any permanent water deficit, *Rinorea* sp. on the other hand showed under the conditions of higher transpiration a steadily increasing permanent water deficit, and rapidly became desiccated. It was noted that when *Rinorea* sp. was established in the tropical houses of the Cambridge University Botanic Garden it grew much more luxuriantly than under natural conditions, which may have been due to these houses having conditions of high humidity and also relatively high light intensity, which latter in the rain forest zone is always associated with increased saturation deficit during the day. The effect might of course have been due to the operation of other factors, such as supply of mineral nutrients.

VI. SUMMARY

1. Observations on atmospheric environmental conditions were made as part of a programme of autecological studies of selected species of the undergrowth flora.

2. The methods which have been used for measuring carbon dioxide concentration in tropical forest undergrowth are examined and previous statements of very high concentrations of carbon dioxide there are shown to be based on insufficient evidence.

3. The concentration of carbon dioxide in the undergrowth of the Nigerian rain forest was not observed to exceed 0.06 % by volume, and thus is of the same order as that in temperate woods. There is a marked diurnal variation, values much above "normal" being recorded only in the morning, there being a steady fall from sunrise to noon. There are no significant differences between the concentrations observed in primary and in 14-year-old secondary forest.

4. These observations agree in general with those of Stocker at Tjibodas in Java. The differences are discussed; Stocker observed a rise in concentration after sunrise. It is shown that his hypothesis of a nocturnal "binding" of carbon dioxide by alkali on the surface of the foliage will not explain this.

5. Data derived from thermohygrograph records of the conditions of temperature and humidity in the undergrowth and tree tops at the end of the dry and the beginning of the wet seasons are given.

6. From the days covered by these data two are selected for more detailed treatment, and the daily march of temperature, of relative and absolute humidity, and of saturation deficit are considered. Comparisons are made between the tree tops and the undergrowth, and between the dry and wet seasons.

7. A similar analysis is given for days at Buitenzorg and Tjibodas in Java and in the neighbourhood of Rio de Janeiro. In general the undergrowth of tropical forest is characterized by a period of saturation during the night, the length of this being very variable, and by a rise of saturation deficit during the morning to a maximum which in no case greatly exceeds 10 mm. Hg and is often much less. There are very small changes in the absolute humidity when the air is not saturated, not only in the undergrowth but also in the open air close to the forest. These small changes, which at Buitenzorg and in the Shasha Forest Reserve are not more than about 2-4 mm. Hg, are in striking contrast to those in the undergrowth of the "Fringing Forest" surrounded by extensive thorn scrub in Northern Nigeria, where at the beginning of the wet season the absolute humidity rises on the average 8 mm. during the day.

8. The difficulties attendant on attempts to survey the conditions of intensity of illumination in forests are discussed.

9. The daily march of intensity of illumination in the undergrowth of primary forest in Nigeria follows a fairly steady course, with few major deviations. Sunflecks are on the whole small both in size and intensity and are confined to a period of about 5 hr. near midday. During this period sunflecks giving a current output from the photocell more than twice that corresponding to the mean shade intensity with the sun unobscured are observed in up to 5 % of the total observations, and those giving more than 5 times only in about 2 % or less.

10. Conditions of illumination in primary and in 14-year-old secondary forest (which has probably passed the darkest phase of the succession) are similar as regards incidence of sunflecks, absolute intensity as measured by the Weston cell, and spectral composition. The secondary forest appears to be on the whole somewhat darker.

11. When the sun is obscured by cloud the intensity of illumination in 14-year-old secondary forest in Nigeria is roughly $\frac{1}{2}$ -1 % of the intensity in the open near the same forest. The ratio is relatively lower with a blue filter, and higher with a red one. This apparent high intensity of red light is probably due to light of wave-lengths greater than 6800 or 7000 Å., in the farther red and near infra-red; presumably in the region of the absorption bands of chlorophyll in the red the intensity is much lower. When the sun is unobscured the spectral distribution is relatively redder in the undergrowth. We have no comparison of total intensities inside and outside the forest under these conditions, but the ratio is probably still about $\frac{1}{2}$ -1 %.

12. These measurements are compared with those of other workers in tropical forests.

13. The possible effects of the environmental conditions observed in Nigeria on the life of the undergrowth plants are discussed.

REFERENCES

- Allee, W. C.** "Measurement of environmental factors in the tropical rain-forest of Panama." *Ecology*, **7**, 273-302, 1926.
- Arens, K.** "Die kutikuläre Exkretion des Laubblattes." *Jb. wiss. Bot.* **80**, 248-300, 1934.
- Atkins, W. R. G. & Poole, H. H.** "Photo-electric measurements of illumination in relation to plant distribution. Part I." *Sci. Proc. Roy. Dublin Soc. N.S.* **18**, 277-98, 1926.
- Atkins, W. R. G. & Poole, H. H.** "Photo-electric measurements of illumination in relation to plant distribution. Part 4. Changes in the colour composition of daylight in the open and in shaded situations." *Sci. Proc. Roy. Dublin Soc. N.S.* **20**, 13-48, 1931.
- Buxton, P. A. & Lewis, D. J.** "Climate and tsetse flies: laboratory studies upon *Glossina submorsitans* and *tachinoides*." *Philos. Trans. B*, **224**, 175-240, 1934.
- Carter, G. S.** "Reports of the Cambridge Expedition to British Guiana, 1933. Illumination in the rain forest at ground level." *J. Linn. Soc. Lond. (Zool.)*, **38**, 579-89, 1934.
- International Critical Tables of Numerical Data, Physics, Chemistry, and Technology.* 1st edition, New York, 1926.
- Lundegårdh, H.** "Neue Apparate zur Analyse des Kohlensäuregehalts der Luft." *Biochem. Z.* **131**, 109-16, 1922.
- McLean, R. C.** "Studies in the ecology of tropical rain forest: with special reference to the forests of South Brazil." *This JOURN.* **7**, 5-54 and 121-72, 1919.
- Moreau, R. E.** "Some eco-climatic data for closed evergreen forest in Tropical Africa." *J. Linn. Soc. Lond. (Zool.)*, **39**, 285-93, 1935.
- Richards, P. W.** "Ecological studies on the rain forest of Southern Nigeria. I. The structure and floristic composition of the primary forest." *This JOURN.* **27**, 1-61, 1939.
- Seybold, A.** "Über den Lichtfaktor photophysiologischer Prozesse." *Jb. wiss. Bot.* **82**, 741-95, 1936.
- Stocker, O.** "Assimilation und Atmung westjavanischer Tropenbäume." *Planta*, **24**, 402-45, 1935a.
- Stocker, O.** "Transpiration und Wasserhaushalt in verschiedener Klimazonen. III. Ein Beitrag zur Transpirationsgrösse im javanischen Regenwald." *Jb. wiss. Bot.* **81**, 464-96, 1935b.
- von Faber, F. C.** *Pflanzengeographie auf physiologischer Grundlage*, von Dr A. F. W. Schimper, 3te Auflage herausgegeben von Dr F. C. von Faber, 2 vols., Jena, 1935.
- Walker, A. C., Bray, U. B. & Johnston, J.** "Equilibrium in solutions of alkali carbonates." *J. Amer. Chem. Soc.* **49**, 1235-56, 1927.

OXIDATION-REDUCTION POTENTIALS IN WATER-LOGGED SOILS, NATURAL WATERS AND MUDS

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(With one Figure in the Text)

INTRODUCTION

ATTENTION has recently been drawn to the existence in soils of potentials measurable at a bright platinum electrode, and it has been suggested that these potentials may be regarded as oxidation-reduction potentials (Pearsall, 1938). The evidence for this view is, in brief, that in a wide range of natural surface soils, the magnitude of the potentials varies (approximately) in accordance with the degree of aeration or waterlogging and also bears some relation to the presence or absence of certain signs of oxidation or reduction. Thus the presence of replaceable ferrous ions could be demonstrated when the potential fell below a certain level (*circa* +320–350 mV. at pH 5). Such soils also gave a negative reaction to the diphenylamine test for nitrates. Above this potential level nitrates were present and iron could only be found in the ferric form. The earlier papers were more concerned with surveying a wide range of soil types than with pursuing these points exhaustively. It is, therefore, desirable to consider other problems connected with the measurement and interpretation of these potentials.

This paper deals with attempts to gain information upon the following specific points:

(a) In the first place it seemed desirable to see if it was possible to define more closely the potential level or levels at which nitrate and ferric iron disappears and below which ferrous iron is found. Field observations upon muddy and sandy soils, showing a wide range of organic content and degree of waterlogging, were undertaken to deal with this point, without danger of disturbance of the natural condition.

(b) Attempts were then made to investigate the same series of phenomena in aqueous solutions, either in mixtures of mud and water or in natural waters. In such mud and water systems under laboratory control it was possible (1) to use oxidation-reduction indicators and to compare the electrode potentials with those indicated by known systems, and (2) to examine the effect of air on these systems.

The discussion of these points is left till later.

METHODS

The methods were as follows. Potentials were determined at a bright platinum electrode, connected to a saturated calomel electrode by a suitable

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saturated potassium chloride (agar) bridge. The potential was measured on a standard potentiometer (Cambridge Instrument Co. Ltd., portable potentiometer). A similar arrangement was used for the determination of pH values in turbid media, soils and muds, using quinhydrone saturated mixtures of one part of mud to two of distilled water. In some cases where natural waters were employed the pH was determined colorimetrically as part of a routine examination. As the various potential values (E_h) were determined at different pH levels, an arbitrary correction is employed (see Pearsall, 1938) which expresses the potential at a constant pH level (pH 5.00). To obtain this value, termed E_5 , for purposes of comparison of various samples, the potential as measured is increased by 58 mV. for every one unit of pH above 5.00, or correspondingly reduced for pH values below 5.00. Thus a potential, E_h , of 200 mV. at pH 6 would be adjusted to 258 mV. at pH 5, and this figure is called the E_5 value. It must be recognized that there is no evidence that this convention is more than an approximation to the true variation of the potential of such systems with varying pH . That it is a fair approximation seems likely by analogy with the data obtained for soils by Willis (1932). In any case this convention has a sounder theoretical basis than the reduction of the potentials to an rH value, which can only justifiably be applied to systems involving the exchange of two electrons. For discussion of this point see Glasstone (1937).

As a test for replaceable ferric and ferrous iron the soil, mud or water was shaken with approximately twice its volume of saturated alcoholic ammonium thiocyanate, allowed to stand for 5–10 min. till the solids had settled, leaving a clear supernatant layer, the colour of which was recorded. One drop of H_2O_2 (10 vol.) was added and any intensification on the colour noted. This is, in effect, Misra's (1938) modification of Comber's test for base-deficiency in soils. The colours are recorded on an arbitrary scale (0–4) as, for example, 2/3, the former figure indicating the original colour produced by the free ferric ions. The latter figure indicates the colour after the addition of hydrogen peroxide which oxidizes any ferrous iron to ferric. The difference in colour is a measure of replaceable ferrous iron. In dealing with natural waters we have also employed the method of Müller (1932) using $\alpha\alpha'$ -dipyridyl as a test for ferrous iron.

The diphenylamine test employed was to add a few drops of a 0.02 % solution of diphenylamine sulphate in pure, concentrated sulphuric acid to a small amount of soil or mud on a white spot-plate and determine whether any blue colour was produced. Diphenylamine, or better diphenylbenzidine, to which it is oxidized in the course of the reaction, functions as an irreversible oxidation-reduction indicator. A blue colour is produced at about +0.76 V. in acid solution. For details see Glasstone (1937). It gives a positive reaction with various oxidizing agents, among others, nitrates and ferric iron. It gives a blue coloration in contact with particles of oxidized soils and muds, possibly reacting with free or adsorbed ferric iron, even though nitrates may be absent. If the reagent is used under the conditions described in this paper, it must be

emphasized that it is not a specific test for nitrate, but an indicator of the presence or absence of oxidizing substances in general. The validity of the numerous field tests for "nitrate" to be found in the literature of plant ecology, in which diphenylamine has been used in a similar manner to that described above, must be doubted. Only when clear soil extracts are tested (cf. Pearsall, 1938) can diphenylamine or diphenylbenzidine be considered to indicate the probable presence or absence of nitrate.

Other determinations were made as part of a routine examination of water samples according to standard methods of water analysis (see American Public Health Assoc.; Standard Methods). Dissolved oxygen was determined by the Winkler method, with no previous oxidation of organic matter or other reducing substances. Ammonia was estimated by direct Nesslerization, nitrate by the phenol-disulphonic method and nitrite with the Greiss-Ilosvay reagents. Sulphide was determined qualitatively with lead acetate, and sulphate, also qualitatively, with barium chloride after concentration of the sample.

RESULTS

(i) *Potential at which iron and diphenylamine are oxidized in soil*

In order to obtain further information on this point, we examined a number of wet soils in the field, to avoid possible alterations of the natural state during sampling and transit. Into a slit made with a pen-knife a spade-shaped electrode was pushed into the soft soil below and the lips of the cut were firmly pressed together. The connection between the soil and calomel electrode was made with a saturated KCl-agar bridge. The potential obtained was usually fairly steady after 5–10 min. and the measurements were recorded after 5 min. In the tables, a sign following the value observed indicates that the potential was unstable and drifting in the direction indicated by the sign. The electrode was left in position while the soil was cut open. A sample from one side of the electrode was taken for *pH* determination, a sample from the other side for the ferric-ferrous tests and a small amount from the same level was smeared on a white spot-plate for the diphenylamine test. All these tests were made on the spot. The observations were then repeated on undisturbed soil close at hand. Usually the electrode was buried at a greater or lesser depth, i.e. in soil levels subject to varying degrees of waterlogging, in order to obtain a series of measurements over the critical range.

Typical results are given in Table I, in which the first series deals with highly organic soils from the swamp at the north end of Esthwaite Water. The second series is from a sandy silt with little vegetation, but with 10–15 % organic matter, by the mouth of a small stream in Sandy Wyke, Pull Wyke Bay, Windermere. The third series is from the margin of a pool on stiff clay with very little organic matter (below 5 %) at Adel, near Leeds. The fourth series is from an inorganic silt by a stream side at Meanwood, near Leeds. This soil is not base-deficient.

Table I. *Potential (E_h and E_s in mV.+) in relation to replaceable iron and diphenylamine test*

Series and locality	No.	pH	E_h	E_s	Diphenyl- amine	Thiocyanate test $Fe^{+++}/Fe^{++} + Fe^{++}$
I. Esthwaite (peaty, subject to varying degrees of waterlogging)	1	5.08	70	78	-	0/3
	2	5.80	105	151	-	1/4
	3	5.30	150	167	-	1/3
	4	4.66	347	326	-	2/3
	5	4.87	340	332	-	2/3
	6	6.21	261 ±	330 ±	-	0/2
	7	5.00	345	345	+	2/3
	8	4.38	361 +	397 +	+	4/4
	9	5.05	417 +	417 +	++	4/4
	10	5.55	415 +	447 +	++	4/4
II. Sandy Wyke (sandy silts, decreasing depths)	11	6.04	205	265	-	1/4
	12	5.92	255	308	-	0/2
	13	5.90	283	335	-	2/3
	14	5.82	365 +	412 +	+	2/2
III. Adel (clay, decreasing depths)	15	5.54	245	276	-	2/4
	16	5.81	290	337	-	2/3
	17	5.50	310	339	-	2/3
	18	4.62	414 +	393 +	+	2/2
	19	4.82	746	466	+	2/2
IV. Meanwood (not base-deficient)	20	7.42	23	163	-	0/2
	21	7.52	38	184	-	0/3
	22	7.50	115	260	-	0/3
	23	7.32	181	315	-	0/2
	24	7.42	237 +	377 +	+	0/0
	25	7.36	256 +	393 +	+	0/0

The table shows that all the soils with a potential of +340–350 mV. at pH 5 (i.e. E_s) give a positive reaction with diphenylamine, but none react for replaceable ferrous iron. The diphenylamine reaction, however, may occur at potentials at which ferrous iron is present (e.g. no. 7), suggesting that the oxidation of diphenylamine proceeds at a lower potential (say $E_s + 340$ mV.) than that at which the iron is wholly oxidized (say $E_s + 350$ mV.). We have observed other indications that this may be the case without obtaining a decisive proof. The explanation of this phenomenon must be left to future research. The theoretical potential at which the blue colour is produced is considerably higher than the range found in the above experiments, even allowing for the difference in pH due to the presence of strong sulphuric acid. The effect of the strong acid on the soil organic matter, possibly on the iron complex, is at present obscure, but presumably important.

It is noteworthy, however, in these and in other results of a similar type, that it is not easy to delimit precisely the potential zone at which the changes, indicated above, take place. This is particularly the case in soils deficient in organic matter. In some observations, not recorded here, carried out on clean river sand, it was found to be extremely difficult to get even approximately stable potentials above about $E_s + 350$ mV. This difficulty may exist in the results shown in Table I, as is shown by the unstable character of the higher values, especially in the less organic soils. While leaving the attempt at the

interpretation of the nature of these potentials to a later discussion, the following points may be made here. It appears probable that organic matter, or some associated system present in the soil, may exert a "poising action" which assists the establishment of an approximately stable potential in the lower part of the range with which we are dealing. The development of marked instability appears to be associated with the range of potential in which the products of oxidation can be shown to exist, and it seems not unlikely, especially in view of later results, that it is associated with the presence of atmospheric oxygen.

Finally series II and III in Table I show that increased oxidation intensity in these samples is associated with increased acidity.

(ii) Potentials in water

Because of the difficulty in soils of delimiting with accuracy the potential zone in which the transition from the oxidized to the reduced condition occurs, attempts were next made to obtain a range of potentials in aqueous mixtures, as it seemed probable that in water a greater range of treatments and reagents could be used. Such systems would further allow of measurement and control of atmospheric oxygen present, and enable the course of other important oxidations, e.g. in the nitrogen and sulphur cycles, to be followed in greater detail. Several variations of method were employed. In the first, each of a number of 100 c.c. flasks was filled with Windermere lake water to which had been added 1 c.c. saturated ferric chloride solution and varying amounts of an organic lake mud ranging from about 2 c.c. downwards. It seemed that most of the ferric iron would be adsorbed by the mud, hence 5 c.c. of saturated alcoholic ammonium thiocyanate were added to some of the flasks in the expectation that ammonium ions would displace the ferric ions from the mud colloids. In actual fact, however, none of the flasks containing mud showed any free ferric ions by the thiocyanate reaction; although, after the addition of hydrogen peroxide, it could be shown in each case that free ferrous ions had been present. Readings for pH and the potential (E_h) are given in Table II.

Table II. *Potentials (mV.+) and reduction of ferric iron in the presence of mud*

Amount of mud	Final pH	E_h	E_s	Fe ⁺⁺
(1) Ca. 2 c.c. + ammonium thiocyanate	3.96	310	251	4
(2) Ca. 1 c.c. + ammonium thiocyanate	4.32	365	326	2
(3) Ca. 0.5 c.c.	4.53	345	318	1
(4) Little	4.70	340	323	1
(5) Trace	5.11	340	346	1
(6) None	5.70	360 +	400 +	0

The results are for four days after the start of the experiment. These figures confirm the conclusion of the previous section, for ferric iron is apparently reduced in these samples only below $E_s + 350$ mV.

It was thought that somewhat similar conditions to those induced in the above type of experiment may exist naturally in the deeper waters of lakes,

provided these are also deficient in oxygen, and especially if sufficient reducing substances, such as organic matter, ferrous iron, sulphides, etc., are diffusing from the mud into the water. During the winter the water of most lakes is kept in complete circulation by wind action, so that atmospheric oxygen entering from the surface and substances diffusing from the bottom muds are distributed uniformly throughout all depths. During the summer, however, the strength of the wind is not sufficient to force the warm surface water down into the colder denser layers below. Circulation thus becomes confined to a surface layer, usually about 10–20 m. in thickness (*epilimnion*), which overlies the colder, denser, stagnating lower water (*hypolimnion*) and is separated from it by a region of sharp temperature fall (*thermocline*). In this way the hypolimnion is cut off from the atmosphere for a long period and, if it contains enough organic matter or receives enough dead plankton from the epilimnion, reduction processes result in a partial or complete consumption of dissolved oxygen. In the extreme cases more reducing substances, ferrous iron, sulphides, etc., may accumulate. The water of Blelham Tarn, containing at least 20 mg./l. of organic matter, is a fairly typical example of a natural water showing this type of stratification. Samples of water, collected from different depths with a Friedinger water sampling bottle, were transported to the laboratory without coming into contact with air. One sample from each depth was used for the estimation of dissolved oxygen. Another was used for potential measurements, while other routine determinations were made on a third. At the sampling locality the water was 11·3 m. deep.

Table III. *Potentials (mV. +) and analytical data (mg./l.) for water at different depths, Blelham Tarn, 19 September 1938*

Depth in m....	0	6	7	8	9	10·3
Temp. °C.	14·5	13·6	13·3	11·8	10·9	10·8
Dissolved oxygen	5·1	4·8	3·6	0·3	—	—
pH, colorimetric	7·3	7·1	6·9	6·5	6·2	6·2
Potential $\left\{ \begin{array}{l} E_h \\ E_s \end{array} \right.$...	374 496	351 461	260 347	220 290	218 288
Total iron	0·04	...	0·32	1·57	3·7	3·7
Fe ⁺⁺⁺	—	—	—	—	—	—
Fe ⁺⁺	—	—	—	1	4	5
NO ₃ '	0·45	...	0·35	—	—	—
NO ₃	Trace	...	0·02	—	—	—
NH ₃	0·08	...	0·08	0·3	0·98	0·86
Sulphate (SO ₄)	+	+	+	—	—	—
Sulphide	—	—	—	—	+	+

Table III shows that the marked oxygen deficiency below 8 m. is accompanied by a low potential and also by the appearance of ferrous iron and of ammonia and sulphide. Only above this level could nitrate and sulphate be detected. In this upper layer, ammonia was present only in traces. The state of the ferric iron was such that its presence could not be demonstrated by the usual ammonium thiocyanate reagent. In our experience the ferric iron is, in the presence of oxygen and under the conditions of pH encountered in these

systems, either precipitated as a complex salt (usually as hydrated ferric oxide) or, if colloidal organic matter is present, a complex is formed with this and free ferric iron can only be detected with the thiocyanate reagent after treatment with acid. The importance of this precipitation, especially in connexion with the phosphorus cycle in natural waters and muds, has been pointed out by Einsele (1938). The mechanism by means of which humus colloids adsorb and transport ferric iron in soils and waters has been demonstrated by various workers. Some general references and a discussion of the practical importance of this type of reaction are given in Waksman (1936).

It appears from the potential values adjusted to pH 5 in Table III that the transitions from the reduced to the oxidized state occur at about a potential of $E_5 + 347$ mV. This agrees with the earlier data obtained for soils (Pearsall, 1938).

A second series of results from water of similar origin is given in Table IV. The collections were made three days later than those in Table III. Attention was concentrated on the critical range in the neighbourhood of the thermocline and samples were taken at depth intervals of 0.5 m. In this case, however, the determinations of dissolved oxygen were made after the potential determinations and on the same samples. In this way it was thought that, even allowing for the oxygen entering the system on the introduction of the electrode and agar bridge, the oxygen values might represent more closely the conditions obtaining at the time of potential measurement. The potential readings are for approximately one hour before the oxygen determinations.

Table IV. *Potentials (mV. +) and analytical data (mg./l.) for different depths, Blelham Tarn, 22 September 1938*

Depth in m....	0	6	7	7.5	8	8.5	9	9.5	10
Temp. ° C.	14.5	13.6	13.3	12.5	11.8	...	10.9	...	10.8
Oxygen	...	6.35	6.0	1.10	0.8	0.6	0.4	0.4	0.3
pH	7.3	7.1	6.9	6.7	6.5	6.2	6.2	6.2	6.2
Potential $\{ E_h$...	390 +	370 +	374 +	375	280	255	220	210
E_5	...	512 +	480 +	473 +	462	350	325	290	280
Ammonia	0.03	...	0.03	0.03	0.07	0.21	0.36	0.45	0.66
Nitrite	-	-	-	+	+	-	-	-	-
Nitrate	0.63	0.77	0.61	0.54	0.29	-	-	-	-
Ferrous iron	-	-	-	-	-	1	3	4	5

Region of thermocline

It will be seen that here again the transition indicated by increased ammonia and ferrous iron, with the absence of nitrate, comes close to an E_5 of +350 mV. It is noteworthy that Pearsall (1938) was also unable to find nitrates in soils below this potential level.

The occurrence of nitrite in the zone of decreasing nitrate and increasing ammonia concentration is of considerable interest. A similar distribution of nitrite, nitrate and ammonia in lakes showing the same type of stratification, involving oxygen depletion, has been found by Müller (1934). Two explanations of the

production of nitrite in this region present themselves. It may be the result of oxidation of ammonia (nitrification), or, it may be produced by the reduction of nitrate. A choice between these alternatives cannot be made from the present data. However, the accumulation of nitrite, both in Tables III and IV, at the top of the transition zone, a metre or so above the level at which the ammonia concentration begins to increase, might seem to suggest that reduction was predominant. The striking similarity between the results described here and those obtained by Müller, a similarity which also extends to the distribution of ferric and ferrous iron, indicates that an analogous stratification may be expected in all lakes with complete oxygen consumption in the hypolimnion.

The value of these observations on lake water, however, lies also in two other features; firstly, that it is now possible to estimate the potentials by both potentiometric and indicator methods, and secondly, because these observations demonstrate a relation between the oxygen concentration of the medium and the potential. It is clear that, in the equilibria or steady states prevailing in these lake waters, the potential $E_5 + 350$ mV. corresponds roughly with the condition obtaining when about 0.4–0.5 mg./l. of oxygen is present, or about 8 % saturation in water at that temperature. In other words, a comparatively low oxygen concentration suffices to maintain predominantly "oxidizing" conditions. This fact is of considerable importance in the ecology of fresh waters, but the main value of the conclusion lies in its relation to soils and muds, in which it is difficult, under natural conditions, to estimate the oxygen concentration. In such cases the potential may be a valuable rough guide to the extent of the influence of oxygen. It is unlikely that a given oxygen concentration will produce the same potential in all cases and under all conditions, since, theoretically at least, the potential must also depend on the ratio of the concentrations of oxidation products to reductants.

(iii) *Estimates of potential with indicators*

As the lake waters used are practically colourless, it is possible to compare the potentials estimated at an electrode with those obtained by the use of suitable oxidation-reduction indicators, a method which is at present impracticable with soils.

The technique employed was to siphon suitable water samples into small (100 c.c.) flasks, completely filling them and adding enough indicator in alcoholic solution to give a distinct and readily detectable colour. The flasks were stoppered, air being excluded, and allowed to stand for one day. The colour reactions of a series of indicators which are reduced (decolorized) at different oxidation-reduction levels (potentials) were then recorded and the electrode potentials determined in the usual manner.

It must be emphasized that the addition of such indicators to mud and water systems involves the addition of a reversible oxidation-reduction

system, which in itself may "poise" the potential of the mixture to some extent. This poisoning action, which is analogous to the buffering of the hydrogen-ion concentration at a certain level, will depend on the difference between the E_0 of the indicator (the potential at which it is half-reduced or half-decolorized) and the potential of the system to which it is added, but also on the relative concentrations of the indicator and the system to be tested. We feel, however, that the concentrations of the indicators added are not sufficient to cause a marked change in the potential of the test system. The fact, that the electrode potentials in Tables V and VI, measured before the addition of the indicator, were in good agreement with the potentials estimated from the indicator tests, supports this view. It should be emphasized that this agreement does not constitute proof that the potentials measured here are truly reversible in the thermodynamic sense. That they are reversible in an ecological sense is pointed out in later discussion. The value of this confirmation of the electrode potentials with indicator measurements lies not in any indication of the mechanism by means of which the potentials are developed, but in the demonstration that electrode measurements, at least in certain potential ranges, do indicate the level of the oxidation-reduction balance of the system, irrespective of the nature of the systems producing this balance. It is further possible in this way to check electrode potentials over ranges where the possibility exists that extraneous factors may influence the potential (e.g. oxygen effect at the electrode surface). Because of these advantages, combined with the extreme simplicity of technique, oxidation-reduction indicators may become tools of considerable value to the ecologist. If a series of indicators is used, potentials may be defined to within 30–50 mV. in most cases; a better definition is not usually possible, as a close enough series of indicators does not exist.

In Table V are given data for samples of water similar in origin to those described in Table IV. These experiments were set up the day after collection. The samples had absorbed a certain amount of atmospheric oxygen during transference to the experimental flask, so they were not in the original condition.

The two indicators used in this experiment are both approximately half-decolorized, i.e. half-reduced, at a potential of +335–340 mV. at pH 5 (Clark, 1928). In the experiment they were approximately decolorized in sample 9.

Table V. *Reaction of samples of known electrode potential with indicators*

No. of sample (original depth in m.)	7	8	9	9.5	10
Colour	{	Phenol blue	Blue	Blue	Pale greenish blue	0	0
		Bindschedler's green	Green	Green	Pale green	0	0
pH			6.9	6.5	6.2	6.2	6.2
Potential in mV.	{	E_A mV. +	318	302	260	250	226
		E_B mV. +	428	389	330	320	296

The potential of this sample measured with the electrode after transference to the experimental flask, but before the addition of the indicator, was $E_0 + 330$ mV. In samples of a higher potential the indicators were not reduced and in samples of a lower potential the indicators were decolorized. Thus the indicator reactions show a potential of the same order of magnitude as the electrode.

Table VI shows the results of another attempt, with a range of water samples, to obtain their reactions with a larger series of indicators. In this case the electrode potentials were estimated before the samples were isolated. The value E_0 is the theoretical value at which the given indicator should be half-decolorized. The E_0 at pH 5 given in Table VI is actually the *known* value at pH 7 plus 116 mV. In a few cases, shown in brackets, the E_0 at pH 5 is known (see Michaelis, 1933).

Table VI. *Reactions of water samples of varying electrode potential with indicators*

Indicator	E_0 at pH 5 mV. +	Water samples			
		1	2	3	4
Orthochlorophenol indophenol	349*	+ +	d		
Orthobromophenol indophenol	346	+ +	d	d	d
Phenol indophenol	343	+ +		d	d
Bindschiedler's green	340 (335)	+ +	d		
Phenol blue	340	+ +	d	d	d
Orthochlorophenol indo 2:6 dichlorophenol	335 (335)	+ +	+		
Phenol indophenol 2:6 dibromophenol	334	+ +	d		
Phenol indophenol 2:6 dichlorophenol	333 (335)	+ +	d	d	d
Metacresol indophenol	324	+ +	+ +	+	d
Orthocresol indophenol 2:6 dichlorophenol	297	+ +	+ +	+ +	d†
Thymol indophenol	290	+ +	+ +		
pH		6.5	6.26	6.25	5.70
Estimated potential by indicators (mV. +)		+ 349	335-324	ca. 324	< 297
Estimated electrode potential at pH 5 (mV. +)		437	327	315	267

+ = full colour; + = colour faint; d = decolorized.

* Unstable at pH 5.

† See below in text.

In these results, as in those given in the previous table, the potential of the samples, estimated by the indicator method, is of the same order of magnitude as that determined potentiometrically. Sample no. 4, while evidently possessing a reduction intensity below that for which most of the indicators were suitable, showed a curious effect with orthocresol indophenol 2:6 dichlorophenol. A definite blue colour appeared at the bottom of the bottle around a slight light brown precipitate. This was most probably a ferric salt (hydrated ferric oxide), which had been precipitated by the addition of a little oxygen during transference of the sample to the experimental bottle. It was apparently maintaining a higher potential in its neighbourhood than that in the rest of the solution.

The rapid precipitation of ferric compounds has been observed in most of these oxygen-deficient lake waters on exposure to the air. It results from the

oxidation of the comparatively large amounts of ferrous iron usually present in them (see Tables III and IV). The presence of these ferric precipitates does not necessarily indicate a potential of above $E_5 + 350$ in the whole liquid. As these compounds are relatively insoluble, and because they are apparently not easily resolvable under natural conditions, they may play no direct part in reversible reactions. If a water with a high reduction intensity and high ferrous iron content, but with a low oxygen concentration, be allowed to take up air, ferric compounds will precipitate out, although the general potential of the remaining aqueous system may be well below $E_5 + 350$ mV. In such a case the insoluble ferric compounds make the system to a certain extent heterogeneous. The rust-coloured films of shiny metallic appearance often seen on the surface of strongly reducing bog waters may represent something of a similar nature, a film of precipitated ferric hydroxide on the surface in contact with the air. In this and similar cases under natural conditions it is often difficult to state whether oxidation had been direct or is the result of microbiological activity.

From the examples given above it will be clear that there is a possibility that a similar heterogeneity may exist at the surface of the electrode, at which there might be a tendency for the formation of oxide films. It is known that such oxide films are formed on the surface of bright platinum in the presence of oxygen and that an irreversible reaction is involved. Hence it is difficult to interpret the behaviour of the so-called "oxygen electrode" (Hoar, 1933), at least in terms of the usual oxidation-reduction theory. It seems important therefore to examine the effect of oxygen (or air) on the type of system we are considering, to see particularly if the electrodes continue to give potentials comparable to those given by indicators when atmospheric oxygen is present and causing the marked drift in potential noted under such circumstances in former experiments (see Tables I and IV).

(iv) *The effect of aeration*

This last group of observations deals with the changes in potential in passing air through samples of water. The arrangement was simple; a flask or bottle containing the water to be tested, was fitted with an electrode, agar bridge and usually a tube to pass air into the bottle. The waters used were either natural lake waters deficient in oxygen or else such waters shaken up with organic mud, allowed to stand in the absence of air and the clear liquid siphoned over into the observing bottle. An indicator was added, the bottle stoppered to the exclusion of air, and sufficient time was allowed for the indicator to become reduced. Air was either allowed to diffuse in from the surface or the bottle was stoppered and air was bubbled through at intervals.

The type of change of potential observed is indicated in Fig. 1 at *A*. On bubbling a small portion of air through the bottle a sudden rise in potential occurs, after which the rise becomes much slower. In the absence of air, the potential will later fall. A further addition of air causes another sudden rise in

potential and by means of such a progressive aeration the potential of the medium can be raised in a series of steps. In this way a potential level may be reached and passed at which an indicator becomes oxidized (coloured). In Table VII are summarized the results of determining the potential when the indicator just began to develop perceptible colour in the vicinity of the electrode. It was not possible to determine the point at which the indicator was

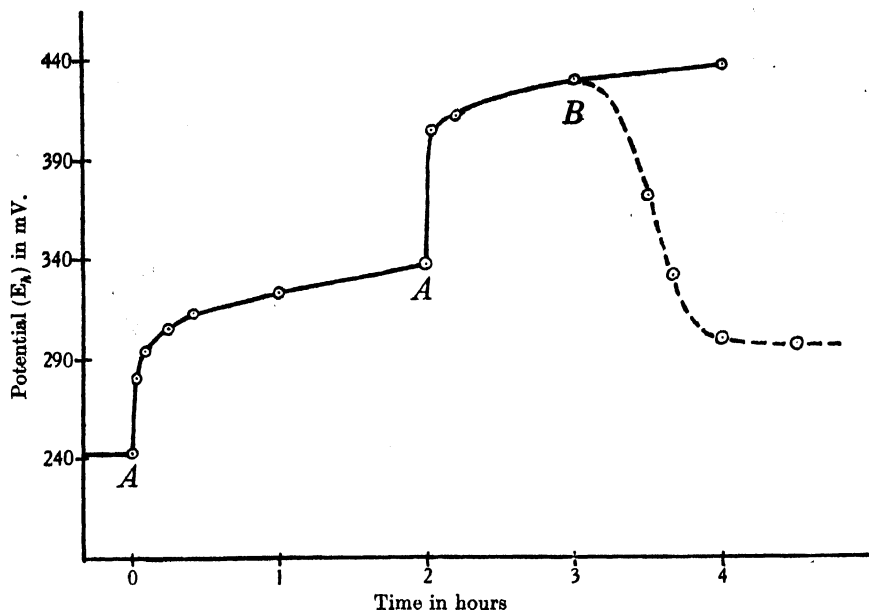


FIG. 1. Changes in potential of an aqueous mud extract, after bubbling air through for 30 sec. at A, and (dotted line) with continuous bubbling of nitrogen from B onwards (*pH* 5.59).

half-oxidized (half-coloured) with any great accuracy. This would of course be the point at which the electrode potential might be expected to agree with the E_0 of the indicator concerned. The agreement, however, is quite good. The last case given in the table does not show close agreement, possibly because it was one of the earliest tests of this type carried out. Further, this last indicator, in common with some others of similar chemical type, turns, in the oxidized condition, from an intense blue to a much fainter pink in the lower regions of *pH* encountered in the systems studied here. Although the effect of reduction on both colours (blue or faint pink) is to decolorize them, the disappearance and appearance of colour in the pink state is much more difficult to follow. This may well explain the discrepancy in the last case in Table VII. When using such indicators, it is sometimes helpful, when circumstances permit, to buffer the *pH* within the range where the blue colour is maintained.

In the above experiments air was bubbled through the observation bottle. In those cases where the contents of the bottle were simply exposed to the air, the same initial rise of potential was noticed on mixture with air. The potential

Table VII. *Potentials in mV. + at point when the named indicator is visibly oxidized*

Indicator	pH of water	E_h	E_s	E_o of indicator at pH 5
Bindschedler's green	{ 6.45	259	343	340
	{ 5.84	299	348	
Phenol blue	{ 5.48	323	351	340
	{ 5.85	289	338	
	{ 6.30	271	346	
<i>m</i> -Cresol indophenol	{ 5.90	277	329	324
	{ 6.42	240	322	
<i>o</i> -Cresol indophenol 2 : 6 dichlorophenol	{ 5.75	255	289	297
	{ 5.94	265	320	

then continued to drift upward at a rate which seemed to be determined by the relative surface exposed to the air. If air be excluded at this stage, the potential again falls. This type of result is shown in Fig. 1, which deals with an experiment in which pond water was boiled to remove oxygen, cooled and mixed with organic mud. After standing in a closed air-free bottle, the clear liquid was siphoned off into the experimental flask, an indicator added and nitrogen (purified over heated copper oxide) passed through for an hour. It was then stood overnight without air when it gave a stable E_h of 243 mV. at pH 5.59. Air was then bubbled through for 30 sec., when the potential immediately rose to 280 mV. and, as the surface was by then in contact with air, continued to rise at a fairly steady rate for 2 hr. When air was again bubbled through, there was another rapid increase of potential (70 mV. in 2 min.) followed by a similar slow steady rise. Up to this point two parallel samples had been treated identically. At this stage pure nitrogen was bubbled continuously through one sample, to remove all traces of oxygen. After an hour of this treatment, the potential had fallen 110 mV. and after 2 hr. it became constant at E_h 294 mV. at pH 5.59 as shown in Fig. 1. It was at the same potential level 15 hr. later.

In this experiment Bindschedler's green was present as an indicator. It was possible to distinguish only three intensities of colour, none, full and intermediate. During the rise of potential during aeration, colour was first noticed when the electrode potential was E_h 312 mV. (pH 5.59). When nitrogen was being passed through, the fading of the colour was noted when the potential was 300 mV. and it had entirely disappeared 20 min. later when the electrode potential was 294 mV. At the pH of this experiment, Bindschedler's green should be half-decolorized at 306 mV. Thus here again, as also in Table VII, the two estimates of potential, by indicator and electrode, show good agreement. And further, the fortunate chance that the final electrode potential (after the removal of air) could be checked by the indicator, enables us to be reasonably sure that no irreversible modification of the electrode has taken place during its exposure to higher oxygen concentrations. From this we do not conclude that irreversible oxide films were not formed at the surface of the

electrode in the higher ranges of oxygen concentration. Indeed it is extremely probable that such was the case (see later discussion). The point demonstrated by the indicator is that, after the removal of oxygen, the reversible function of the electrode is reinstated. If this is so, then it appears from Fig. 1 that besides the effects which were associated with the introduction and removal of oxygen, a change had taken place in the solution. The final stable potential was higher than the original one. Thus of a total rise of 188 mV., 53 mV. remained after the removal of oxygen. It is suggested that this may represent oxidation products in solution.

Note on the oxidation-reduction potentials in lake muds

As the distribution of oxidation-reduction potential in lake muds presents points of special interest in other connexions, one of us (C. H. M.) proposes to publish more detailed results in another communication. The brief treatment accorded to muds here simply serves to show that we are apparently dealing with similar systems to those already described for waterlogged soils and reduced natural waters. In fact the reduced hypolimnion of a lake can be considered to be part of the mud system in the larger sense, as a large part of the reducing substances found in the water have their origin in the mud.

If an organic, reducing mud containing iron is covered with water in a jar and exposed to the air, a brown layer of lighter colour than the underlying mud, at most of a few millimetres thickness, will form on the mud surface after several days. Table VIII shows the distribution of potential and of the products of oxidation and reduction in such a system. In similar experiments it has been found that the change in the colour of the surface mud from black to lighter brown is due to the precipitation of ferric compounds and is first observed at a potential in the neighbourhood of $E_5 + 340$. The distribution of oxidized and reduced substances in relation to this potential zone appears to be identical with that found for soils and reduced waters (see Tables I, III, IV and VIII). This is regarded as evidence that similar systems influencing potential are present in all cases.

The surface oxidized layer is readily detectable on most lake muds in the field if care is taken to preserve it during sampling. It disappears if conditions

Table VIII. *The distribution of potential (E_5 mV. +) and of products of oxidation and reduction (mg./l.) at the water-mud interface. Windermere mud (from 52 m. depth) standing under water exposed to air in laboratory*

	Appearance	E_5 mV. +	Diphenyl- amine	Thiocyanate		Filtrate			
				Fe ⁺⁺⁺	Fe ⁺⁺	NO ₃	NO ₂	NH ₃	Sulphide
Water above mud	...	461	...	Trace	-	1.0	-	0.03	-
Surface 3 mm. mud	Brown, flocculent	374	+	+	-	3.2	Trace	0.17*	Trace
Lower mud	Black	115	-	-	+	-	-	1.68*	+

* Only a small proportion of the total adsorbed value.

in the hypolimnion become reducing. This layer may be of considerable importance in controlling exchange of substances between the water and the mud.

DISCUSSION

In this paper we are concerned with the description of facts rather than with their interpretation. Nor is any attempt made to draw parallels between the potentials measured here and the magnitude and suggested nature of potentials observed in other systems such as solutions of pure substances, bacterial cultures or tissue extracts. The behaviour of the potentials in various potential ranges has, however, suggested certain interpretations to us. These are put forward here, however, only in the form of a very generalized working hypothesis, which it is hoped will prove a basis for a more detailed experimental investigation of the systems which influence the potential in natural waters, muds and waterlogged soils. We are concerned here with emphasizing the ecological significance of the facts put forward. In the measurement of potential we have a method of showing whether a soil or a natural water system is capable of oxidation or otherwise, under conditions where direct oxygen measurements are inconvenient or impracticable. Further, in many cases it is probable that the oxidation-reduction potential, i.e. a value which indicates the general level of oxidation or reduction of a system, is a factor of greater biological significance than oxygen concentration alone.

The results suggest that approximately stable, reproducible potentials can be demonstrated in soils and muds over a wide range and in natural waters at least in a zone between 250 and 350 mV. at pH 5. In all cases so far examined, in soils, waters and muds, representing a wide variety of natural conditions, products of oxidization (ferric iron, nitrate, sulphate) are found above the potential zone $E_5 + 350$ mV.; below this potential their reduced counterparts (ferrous iron, ammonia, sulphide) are present. From this it would appear likely that the mechanism of potential formation in all three types of system, soil, mud or water, is similar in nature. Of great ecological interest is the demonstration that the change-over from "reducing" to "oxidizing" conditions (at $E_5 + 350$ mV.) in natural water systems takes place at relatively low oxygen concentrations (8 % saturation or less). It seems likely, therefore, that, in water, muds and soils, a relatively low oxygen concentration suffices to maintain predominantly "oxidizing" conditions. These potentials are affected by the oxygen concentration of the medium, and the results with air and nitrogen in watery mixtures seem to explain the upward drifts of potential observed in soils on disturbance (Pearsall, 1938) as related to increased oxygen concentration. They would also serve to justify the explanation on these lines of the effects of closer packing and increased water content. The downward drifts of potential in disturbed muds (Misra, 1938; Pearsall, 1938) are probably correlated with oxygen consumption.

A second important feature of the observations on water systems is that potentials outside an approximate range $E_5 + 350$ –200 appeared to be much more sensitive to the conditions under which the observations were made than potentials within that range. They frequently, if not always, showed a marked tendency to drift and were extremely sensitive to slight polarization such as may occur in balancing the potentiometer. These conditions are regarded as evidence of "instability" and must be taken into account in any attempt to interpret the nature of these potentials. The instability in the potential range above $E_5 + 350$ mV. is thought (see later discussion) to be due to the presence of oxygen. The lack of an effective "poising" system and the prevalence of irreversible reductions may be the explanation of the behaviour of the potentials in the lower region. It is possible that sulphide systems may be important in this region. Such factors may also be partly responsible for the large drifts in potential observed in muds brought into the laboratory, when the steady state or equilibrium existing in nature is disturbed by such factors as changes of temperature, and the entry of air during sampling, transport and the insertion of the electrode.

The fact that oxygen is not excluded from the usual measurements means that we have to consider two possibilities: (1) the potentials which would theoretically be developed at a reversible oxygen electrode in water and (2) the probability that the potentials actually measured by bright platinum electrodes in the presence of oxygen include the effects of irreversible oxide films formed on the electrode surface. The difficulties in the way of the theoretical treatment of such an oxygen electrode have long been recognized. Hoar (1933) concluded that the irreversible nature of the potentials lies not so much in the formation of the oxide films as in their porosity and permeability to the electrolyte which results in self-polarization of the electrode.

From recent physical-chemical data Cooper (1938) has calculated the theoretical oxidation-reduction potentials given by a reversible oxygen system under various conditions in sea water. Under natural conditions this would lie between +0.7 and +0.8 V. In view of our findings that a marked fall in potential, in other words, the change-over from "oxidizing" to "reducing" conditions, only takes place at low oxygen concentrations, it is of interest to note that Cooper's calculations show that a fall in oxygen concentration from 100 to 10 % saturation involves a fall of only about 15 mV. in the theoretical potential of the oxygen system.

The practical difficulties in the way of measurement of potential at an oxygen electrode and the irreversibility of such potentials have been outlined above. They explain the instability of such potentials and the great differences in potential values obtained in oxygen systems by different workers. Hoar (1933) has obtained results which he considers typical of bright platinum electrodes under good working conditions. From these data Cooper (1938) has calculated the irreversible potential of an oxygen electrode in water for various

pH values. Actual measurements on natural and acidified sea water showed a better agreement with these calculated values than might have been expected. It appears then that the potential at a bright platinum electrode in sea water (*ca.* +0.43 V. at *pH* 8.15) is governed solely by the irreversible oxygen system. Heintze (1935) arrives at a similar conclusion for various soil solutions.

The theoretical treatment for sea water can be extended to all aerated natural waters if no reducing substances or other poisoning systems are present. In considering such waters as ecological and physiological environments Cooper points out that potentials of importance to the organism must lie between the theoretical potential for the reversible oxygen system and the (lower) irreversible potential at the oxygen electrode. In no case will the oxygen system function strictly reversibly, but on the other hand the organism cannot be considered to react in the same way as an irreversible electrode forming porous oxide films. In the presence of high oxygen concentration it is at the moment impossible to define the potential in natural water within closer limits than this. No truly reversible oxidation-reduction indicator exists for this range of potential. For practical purposes it will be sufficient to calculate the reversible potential from the reversible oxygen system formula and to obtain the irreversible potential by graphical extrapolation from Cooper's data. In this way an irreversible oxygen electrode potential of *ca.* +600 mV. is obtained for *pH* 5. This is about the maximum figure recorded for natural soils, while our measurements in natural waters rarely exceeded $E_0 + 500$ mV. (see Tables III and IV). This may possibly be explained by the presence of traces of reducing substances or of other poisoning systems in concentrations much higher than in sea water.

From the above considerations it appears evident that the potentials of the surface waters of lakes, and indeed all natural waters with a high oxygen and low organic content, is governed largely, if not wholly, by the irreversible oxygen system. The lower waters of some lakes, where conditions during the summer cause the oxygen content to be depleted, show much lower potentials in virtue of their low oxygen tension and the presence of reducing substances and poisoning systems probably associated with decomposing organic matter. The similarity between the conditions obtaining in such reduced waters and in reduced muds and soils—a similarity which extends not only to the magnitude of the potential, but also to its relation to the appearance and disappearance of recognizable products of oxidation or reduction—has been pointed out on previous pages. The interpretation of the nature of the potentials observed in such systems is considerably more difficult than in the case where pure water and oxygen alone constitute the oxidation-reduction system. These difficulties depend largely on our ignorance of the systems really involved.

We suggest as a basis for a working hypothesis that the actual potential observed may be affected by three main factors or groups of reactions.

First, it seems likely that truly reversible systems, in the sense required by

oxidation-reduction theory, are present in natural soils, muds and waters, and that these systems give effective concentrations of oxidation and reduction products, of which the ratio of the concentrations (activities) influences the potential.

Secondly, it is probable, in such complex organic systems, that irreversible oxidations and reductions take place as well. Reactions of this type are well known in biochemistry. In many irreversible oxidations the primary oxidation product undergoes spontaneous irreversible change in such a way that the reduced phase alone influences the potential which is unstable and may fall to a very low value. In theory, in aqueous solutions, it should approach the hydrogen electrode potential for the pH of the medium. That it does not do so in all cases is due to other reactions and the inertia of the potential-forming mechanism at the electrode surface. For a more detailed discussion see Michaelis (1933). In practice the potential approaches, more or less asymptotically, a steady state ("Grenzpotential": Michaelis) which is unstable, but reproducible within certain limits under identical conditions. The final potential level is determined by such factors as the concentration of the reduced phase concerned, the poisoning action of other systems which may be present, the rate of diffusion of oxygen into the system, etc. It represents, not a thermodynamic equilibrium, but a kinetic steady state depending on the relative rates of various reactions. The way in which some potentials are developed in the systems we have been considering, especially in reducing muds, suggests that the potentials in the "unstable" ranges may be determined largely by such mechanisms as described in this paragraph. It will be the task of future work to discover whether such an interpretation is correct.

Thirdly, it seems certain that oxygen, if present, will influence the potential. This influence may be a direct effect on the electrode surface, as discussed above, or indirect through the changes brought about by oxygen in the equilibria or steady states produced by the first two types of reaction.

Little evidence is available in the present communication to indicate the relative importance in the different parts of the potential range examined of the three factors mentioned above. The influence of oxygen has been dealt with in some detail, but the relative influence of reversible and irreversible reactions in other ranges is still obscure. It is, however, worth pointing out that whether the systems examined involve reversible or irreversible reactions, in the thermodynamic sense, or not, they are reversible in an ecological sense. It is this aspect of their importance which it is desired to emphasize at present.

SUMMARY

1. The attempt is made to correlate with other properties the potentials developed at a bright platinum electrode in soils, muds and natural waters.
2. In wet soils and muds, the diphenylamine reaction is positive and replaceable, ferrous iron disappears above a potential of 350 mV. (approx.) at pH 5.

3. In natural waters, ferrous iron is only detectable below this potential, while below the same point ammonia tends to replace nitrate and sulphides to replace sulphates.

4. In these waters, this potential is found at low oxygen concentrations, equivalent to about 8 % of saturation, or less.

5. The apparent potentials estimated with various oxidation-reduction indicators agree with the electrode potentials in the critical range.

6. Data are given for the effects of oxygen on the drifts of potential.

7. The potentials appear to be related to ecologically reversible systems and suggestions are made as to their physico-chemical nature.

REFERENCES

- American Public Health Association.** *Standard Methods for the Examination of Water and Sewage*, 8th ed. New York, 1936.
- Clark, W. M.** *The Determination of Hydrogen Ions*. London, 1928.
- Cooper, L. N. H.** "Oxidation-reduction potentials in sea water." *J. Mar. Biol. Ass.* **22**, 167, 1938.
- Einsele, W.** "Über chemische und kolloid-chemische Vorgänge in Eisen-Phosphat-Systemen." *Arch. Hydrobiol.* **33**, 361, 1938.
- Glasstone, S.** *Oxidation-reduction Potentials and their Applications*. Institute of Chemistry, London, 1937.
- Heintze, S. G.** "Soil oxidation-reduction potentials and pH values." *Bodenkundliche Forschungen*, **4**, 351, 1935.
- Hoar, T. P.** "The mechanism of the oxygen electrode." *Proc. Roy. Soc. A*, **142**, 628, 1933.
- Michaelis, L.** *Oxidations-reduktionspotentiale*. Berlin, 1933.
- Misra, R. D.** "Edaphic factors in the distribution of aquatic plants in the English lakes." *This JOURN.* **26**, 411, 1938.
- Müller, H.** "Die Verwendung von $\alpha\alpha'$ -Dipyridyl zur Bestimmung von Ferro- und Gesamteisen in natürlichen Wässern." *Mikrochemie*, **12**, 307, 1932.
- Müller, H.** "Über das Auftreten von Nitrit in einigen Seen der Österreichischen Alpen." *Internat. Rev. Hydrobiol.* **30**, 428, 1934.
- Pearsall, W. H.** "The soil complex in relation to plant communities: I, II, III." *This JOURN.* **26**, 180, 194, 298, 1938.
- Waksman, S. A.** *Humus*. Baltimore, 1936.
- Willis, L. G.** "Oxidation-reduction potential of a soil." *J. Agric. Res.* **45**, 751, 1932.

571-575

THE VEGETATION OF "SCREES" IN CERTAIN HILL GRAZING DISTRICTS OF SCOTLAND

By E. WYLLIE FENTON

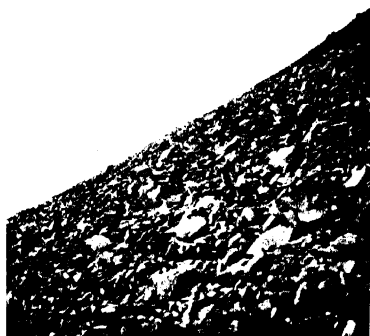
(With Plate XXVI)

IN Scotland any bare area on a hillside which consists of stones, rubble, or a mixture of these and of pieces of rock is generally called a "scree". The writer has also met with the very apt expression of "bare-faces" for "screes". These "screes" are not the typical "screes" at the foot of a rock face, the talus of the geologists, but in most cases they are due to erosion. It is not feasible to call them erosions, because erosion may not lead to "screes" but may still show soil or subsoil, if these are of reasonable depth. Hence in this paper the term "scree" will be used in the Scottish and not the orthodox usage. Generally, these "screes" are not individually of great extent, but within any grazing district the grand total may reach a considerable acreage. Hence some knowledge of their origin and vegetation is important.

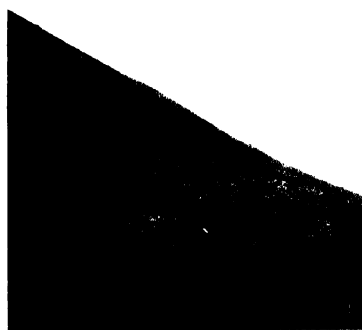
When soil loses its vegetation covering, the speed with which that area is recovered is frequently a very important matter. Where there is no adequate covering of vegetation there is of course great danger of soil erosion. Soil erosion in some countries has become a national calamity. In Britain—so far—soil erosion of an extensive nature incurring heavy financial loss is fortunately rare. The sand dunes at Fowie, and the famous Culbin Sands on the Moray Firth, are two well-known and historical examples of past negligence and destruction. In hill land and mountainous districts, soil erosion may often lead to scree formation or to re-exposure of old scree surfaces. Perhaps the most common form of wastage is on hillsides or on sloping heaths where fire destroys the vegetation, and the thin soil or peat erodes, leaving a bare surface of stones (Wallace, 1917). Other sources of similar wastage may be caused by rabbit burrows, and sheep breaking the surface of the hillside to form scratching holes. From these two sources wastage may spread down the side of a hill, and extend laterally, till a considerable area is affected (Fenton, 1933-7). Where no fire may have occurred, excessive moisture, or the action of frost or heavy rain, may cause a weakness at any part, and a small landslide may begin and spread. Hence one finds steep screes and rock faces with little or no vegetation except perhaps lichens and a few mosses. On examination, it is often evident that a scree of stones has been formed within comparatively recent times. The presence of partially buried stems of juniper, birch, etc. (*in situ*) clearly indicates that a small landslide or erosion has occurred. The wastage of soil has led to the downward wash of stones and small fragments of rock so as to bury, or partially bury, the vegetation of a lower level. This is a common occurrence in the southern uplands of Scotland.



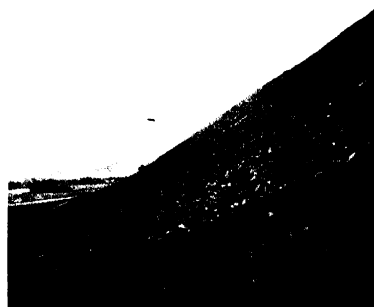
Phot. 1.



Phot. 2.



Phot. 3.



Phot. 4.

Phot. 1. Scree formation, following tree felling, and soil erosion.
Phot. 2. A bare part of Cademuir scree.
Phot. 3. Part of a covered scree, north side of Cademuir.
Phot. 4. Part of Cademuir scree, *Pyrus communis* near skyline.

WYLLIE FENTON—THE VEGETATION OF “SCREES” IN SCOTLAND

After the formation of a scree, how is it clothed with vegetation? This is not an easy question to answer, as in many if not in most instances, a complete covering would not occur in one lifetime. The only way to attempt to overcome this difficulty is to investigate a large number of screes and then piece together the various stages of vegetation covering which develop. For the most part (at lower elevations), typical screes generally occur where heather held a thin covering of peat, or peaty soil, in position on the hillside, or near the summit. Once a break occurs the area may rapidly extend, and with the wasting of the peat a scree of small stones or rocks is left with no vegetation.

In the present study the screes considered are situated either in the Pentland Hills, or the northern part of the Moorfoots. The average elevation would be about 1000 ft. (300 m.). All the rocks are of igneous origin, from which the screes are derived. These screes, of course, differ both in extent, position and slope.

Some rocks are basic while others are acid, but no significant difference was observed on the screes examined. A slope with a northern exposure does not get the heat of the sun like the southern exposure, and on that account may succeed more quickly in forming a covering, or a partial covering.

The following are a few examples of screes and the vegetation present. All lie between 800 and 1000 ft.:

No. 1, a scree in the southern uplands with north-west exposure. There were a few lichens, but not many. *Racomitrium heterostichum*, *R. lanuginosum*, a few plants of *Festuca ovina* and *Agrostis vulgaris*. Soil erosion is the cause of this scree, but there is no satisfactory evidence as to whether it followed burning of heather.

No. 2, another small scree with a gentle slope, had only two mosses present: *Polytrichum urnigerum* and *P. juniperinum*. A good collection of dust and fine soil had accumulated between and on the stones. The exposure was south-east. Although there is not strong evidence, this scree probably followed heather burning.

No. 3, a small scree in the Pentlands, revealed only two mosses: *Dichodontium pellucidum* and *Dicranum scoparium*. These two mosses appear only near the foot of the scree. There is no evidence of heather burning, so a local landslide or break may be the cause of erosion.

No. 4, a scree near a stream in the southern uplands, was chiefly clothed with *Racomitrium canescens*. There were also present: *Hypnum Schreberi*, *H. cuspidatum*, *Dicranum scoparium*, *Polytrichum juniperinum*, a little *Grimmia* spp., *Peltigera canina*, *Festuca ovina* and *Agrostis vulgaris*. From other parts near it was evident that *Racomitrium canescens* was the pioneer. The nature of the surrounding district suggests that, in the past, heather burning possibly led to erosion, but there is no satisfactory evidence.

No. 5, a scree in the Pentlands with a north-eastern exposure, had as its chief growth *Racomitrium lanuginosum*, but near the base *Dicranum scoparium*

occurred, and also patches of *Calluna vulgaris* and *Pteridium aquilinum*. *Calluna* had seemingly commenced from seed on some of the dust and from peat fallen from above, but the presence of bracken was difficult to explain. There was no bracken sufficiently near the base, and it did not seem to be coming through the depths of the scree, so probably some piece of rhizome with soil attached was washed down from the higher ground and commenced growth. This is by no means an uncommon commencement of a vegetation covering. Growth starts near the base of the scree, and provided the slope is not too steep it moves slowly up as well as in a downward direction. In this example heather burning contributed towards erosion, if it was not the primary cause.

No. 6, a scree in the Pentlands with a south-western exposure, revealed the presence of *Rhacomitrium lanuginosum*, the dominant species, *Polytrichum formosum*, *Hypnum cupressiforme*, *Deschampsia flexuosa* and *Festuca ovina*. This is another example of erosion following the burning of heather.

No. 7, a scree in the Pentlands with a western exposure, had a vegetation of *Rhacomitrium lanuginosum* (chiefly), *Hypnum cupressiforme*, *Agrostis* spp., *Festuca ovina* and *Holcus lanatus*. Colonization has proceeded farther than in most screes, and no evidence is left of the cause of erosion.

No. 8 is a very interesting scree in the Pentlands with a southern exposure, and contained the dead stems of juniper appearing just above the line of the scree. The chief plant was *Teucrium Scorodonia*, and *Cytisus scoparius* was plentiful. The two mosses *Rhacomitrium lanuginosum* and *Hypnum cupressiforme* were present, and also *Agrostis* spp., *Festuca ovina*, *Holcus lanatus* and *H. mollis*. In the present example *Teucrium Scorodonia* was most active in fixing the scree and in parts formed a complete covering. It was noted that *T. Scorodonia* was not common in the vicinity. *Cytisus scoparius* also did not occur near the scree, and must have been introduced from some other district. There is little doubt that this marks the site of a retrogressive wood or scrub growth. The destruction of this by fire or other agency led to erosion.

No. 9, a rather interesting scree in the Pentlands, showed the lichens *Physcia coesia*, *Lecidea granulosa*, *Lecidea* spp. and *Rhizocarpon geographicum* on the stones. *Parmelia physodes* was present in quantity and also *Cladonia rangifera*. On decaying pieces of *Calluna* stem *Cladonia macilenta* was present as well as *C. pyxidata*. The dead stems of *Calluna* had been washed down from the higher ground. During wet spells *Hormidium* (*Prasiola flaccidum*) occurs in quantity. *Ulothrix zonata* also appears at times. Where remains of mosses, dust and debris accumulate, and occasionally on a cushion of moss, grasses such as *Deschampsia flexuosa*, *Festuca ovina*, *Agrostis vulgaris*, *A. canina* and *Nardus stricta* occur. *Holcus lanatus* and *Poa annua* were occasionally found. Mosses certainly seemed to gain a footing much more readily where lichens or occasionally algae prepared the way. Grasses always appeared at a later stage. The mosses present were *Polytrichum commune*, *Hypnum cupressiforme* and *Webera nutans*. This area had probably been covered by a heathy

vegetation with juniper, as traces of the bushes may still be found. Probably burning led to total destruction of surface vegetation and erosion followed.

No. 10, a scree stretching to the top of the hill, gave a very interesting succession. The scree had been caused by a severe heather burn. After wastage, only a bare area of stones and broken small pieces of rock remained. All the stones were bleached and, certainly on the surface, partly disintegrated. There remained a few tufts of soil with *Deschampsia flexuosa*. Even these had till recently decreased in number by undercutting, and had rolled down the hill. On the bare spaces of considerable extent the first noticeable vegetation was *Hormidium* spp. and *Ulothrix zonata*. Mosses have not yet played any role in the plant succession, though some moss protonema and traces of moss were found (*Hypnum* spp.). Then followed *Rumex acetosella*, *Festuca ovina* and, later, *Agrostis* (*vulgaris* and *canina*). Later plants of *Poa annua* and *Holcus lanatus* were found. The last two were introduced by sheep. Patches which were bare a few years ago are now covered, but the success of this covering will depend very largely on the absence of a severe drought. The interesting feature of this scree is that neither lichens nor mosses played any important role. The absence of the former is doubtless due to the constant wastage and breaking down of the surface of small pieces of rock and stones. The marked absence of moss is unusual and is not easy to explain. It may be due to the same cause which prevents lichens making progress. At a later date a considerable quantity of *Aira praecox* appeared.

No. 11, a very interesting scree with a southern exposure, occurs on Cademuir, near Peebles (see Photos. 2, 4). The lichens identified were *Phycia coesia*, *Lecidea* spp., including *L. granulosa* and *L. contigua*, *Rhizocarpon geographicum*, *Parmelia physodes* and *Peltigera canina*. Mosses present were *Rhacomitrium lanuginosum*, *Hypnum Schreberi* and *Hylocomium triquetrum*, *Hypnum cupressiforme* and *Dicranum scoparium*. Other plants were *Galium saxatile*, *Viola canina* and *V. lutea*, *Agrostis canina* and *A. vulgaris*, *Festuca ovina*, *Holcus lanatus* and *H. mollis*, *Oxalis acetosella*, *Veronica serpyllifolia*, *Teucrium Scorodonia*, *Mercurialis perennis*, *Pteridium aquilinum*, *Lastrea filix-mas*, *Digitalis purpurea* and *Thymus Serpyllum*. There were also a few clumps of *Prunus communis* and one *Crataegus oxyacantha*. The contents of this scree will be dealt with in the discussion to follow. It is of interest to point out now the presence of several plants which are often associated with open woodland. There is no doubt that this scree is the site of a retrogressive wood destroyed many years ago.

No. 12, a scree derived from an open woodland with a ground vegetation of *Calluna vulgaris* and *Vaccinium myrtillus* in quantity, gave the following flora: *Festuca ovina*, *Nardus stricta*, *Deschampsia flexuosa*, *Holcus mollis*, *Galium saxatile*, *Calluna vulgaris*, *Vaccinium myrtillus*, *Oxalis acetosella*, *Dicranum scoparium*, *Hylocomium triquetrum*, *Hypnum cuspidatum*, *Rhacomitrium lanuginosum*, *Teucrium Scorodonia*, *Viola canina* and *V. lutea*, *Hypericum humi-*

fusum and the three ferns *Polystichum aculeatum*, *Polypodium dryopteris* and *Lastrea filix-mas*. Rabbits and sheep (especially rabbits) were causing continued wastage on the fringes where *Galium saxatile* was the most important soil-binder. In parts, *Rhacomitrium lanuginosum* was playing the chief role in filling up gaps between the stones and rocks and in covering the stones. On this medium grasses were slowly spreading.

No. 13: the following brief description of an example of the colonizing of a deforested hillside, which might have developed into a scree, is rather interesting. The slope is steep and faces north. The top of the hill is still covered with *Calluna vulgaris* and a thin covering of peat. There are plantations on the western side. About twenty years ago, the rather open tree covering of Scots pine was felled and removed. The original vegetation beneath the trees, although varying from place to place, consisted essentially of patches of *Vaccinium myrtillus*, *Hylocomium splendens*, *Hypnum Schreberi* and *H. cupressiforme*, all plentiful. Present to a lesser extent were *Deschampsia flexuosa*, *Festuca ovina*, *Hylocomium triquetrum*, *Galium saxatile*, *Dicranum scoparium*, *Viola canina*, isolated patches of *Empetrum nigrum*, *Oxalis acetosella* and *Calluna vulgaris*, and in one restricted area *Anemone nemorosa*. It was evident that *Calluna vulgaris* had been more plentiful in the past. In a few parts there were patches of *Pteridium aquilinum*, while in the more open parts where trees were more widely distributed was a grassy ground vegetation of *Festuca ovina*, *Deschampsia flexuosa*, *Agrostis vulgaris*, *A. canina*, *Holcus lanatus* and *H. mollis* (chiefly the latter), *Galium saxatile*, *Hypnum Schreberi* and *Hylocomium squarrosum* (both plentiful), *Dicranum scoparium*, *Polytrichum commune*, *Hypnum cupressiforme*, *Hylocomium triquetrum* (locally common), *Viola canina*, *Campanula rotundifolia*, *Veronica serpyllifolia*, *Anthoxanthum odoratum* (a little) and *Luzula campestris*. Small isolated patches of *Peltigera canina*, *Cladonia* spp., *Potentilla Tormentilla*, *Polygala vulgaris*, *Veronica Chamaedrys* were also present.

With the felling and removal of the trees most of the ground vegetation in the steep part was destroyed. In a few isolated spots small screes began to form, and there was distinct soil erosion. Later there was for a few years a luxurious growth of *Ptilidium ciliare* over considerable parts of the felled area. This hepatic played a very important part in fixing the surface soil and arresting erosion. It is one of the few examples found where a hepatic has played the chief role in arresting soil erosion leading to scree formation. This could only have occurred on a shaded northern slope. The next two plants which played an important part were *Galium saxatile* and *Deschampsia flexuosa*. At this stage all danger of serious erosion had passed and mosses and grasses spread rapidly. *Festuca ovina*, *Agrostis* spp., *Holcus mollis*, *H. lanatus*, *Hypnum Schreberi* and *H. cupressiforme* filled up any gaps, while *Cladonia* spp. and *Peltigera canina* also helped. In the drier parts *Potentilla Tormentilla*, *Hylocomium squarrosum* and *H. triquetrum*, *Dicranum scoparium* and *Polytrichum*

spp. to a lesser extent filled up any bare spaces. In one or two places *Teucrium Scorodonia* occupied much of the ground. In a short time the vegetation will be quite typical of the heathy type of grassland so common over much of the Scottish southern uplands.

No. 14, a scree on the north side of Caerketton, is a good example of one formed chiefly by a talus. Small parts of this scree have some vegetation. Most interesting is the fact that *Urtica dioica* and *Poa annua* are both assisting to bind parts of the loose rubble of stones. These two plants have been introduced by sheep and rabbits. Other plants playing a part were *Hormidium* spp., most of the lichens already noted elsewhere, *Bryum* spp., *Polytrichum commune*, *Dicranum scoparium*, *Deschampsia flexuosa*, *Oxalis acetosella*, *Calluna vulgaris*, *Vaccinium myrtillus*. On the fringes of the scree was a vegetation typical of heathy upland areas. Among the plants found were *Oxalis acetosella*, *Luzula sylvatica*, *Plagiothecium undulatum* and *Lophozia Floerkii*.

DISCUSSION

The vegetation of true screes has already been considered by Leach (1930) in this *Journal*. This author also dealt with the very meagre British literature and also work done on the continent of Europe. Conditions in the Pentland Hills and the northern part of the Moorfoot Hills are not quite similar, but make an interesting comparison. The climate is different to that of the Lake District already investigated. In the Pentland Hills and the Moorfoot Hills, the climate is markedly that of the east coast—comparatively dry, often cold east winds and bright sunshine. Drought on a small scale frequently occurs. Many of the screes examined are derived from rocks of metamorphosed sandstones and grit or of igneous origin, and most of them are acid, although a few are of basic (but non-calcareous) material. The soil from basic rocks is generally acid, due to leaching. The change from one to the other is at times quite sudden. An example of this is to be found in Boghall Glen (Fenton, 1933). In spite of this change in the nature of the rock, the screes examined did not show any marked difference in vegetation. This suggests that, in the area investigated, climate and exposure are more important than the composition of the underlying rock.

From the examples quoted it is evident that the flora of the screes examined is generally much more restricted than those described by Leach (1930, 1931), Evans (1932) or Watson (1925, 1932). The differences in climate and geographical position may be important factors.¹ It will be noted, however, that *Rhacomitrium* spp. play an important part, especially *Rhacomitrium lanuginosum*, while *Hypnum cupressiforme* is also frequent. This is more in keeping with certain conditions in Caithness as described by Crampton (1911). The

¹ Dr J. B. Simpson of the Geological Survey informed me that many screes in the south-west of Scotland have large quantities of Parsley Fern (*Allosurus crispus*). This fern helps to fix the scree (cf. Leach, 1930).

frequent occurrence of *Deschampsia flexuosa*, *Festuca ovina*, *Agrostis vulgaris* and *A. canina* also suggest very similar conditions to those described by Crampton (1911).

Considering the fourteen examples quoted, it seems that apart from no. 14 all the others are probably due to erosion. In many places there are indications of heather (*Calluna vulgaris*) burning, long after the burn has occurred. There are, however, examples where it is not possible to find any conclusive evidence, such as nos. 1, 3, 4 and 7. Nos. 2, 5, 6 and 10 are examples of erosion after heather burning.

The steeper the slope the greater the danger of erosion. Nos. 8, 9, 11, 12 and 13 are typical examples of erosion following the destruction or removal of trees on a sloping hillside. No. 14 is the only example of a true scree or talus. On many of these hillsides the soil, peat or peaty soil may be very shallow, two inches or less is quite common and occasionally it may be slightly less. Consequently a severe burn or the removal of trees, may readily destroy the soil covering and leave a bare scree of stones, or rock. Erosion may, however, be due to natural causes. Excessive rain and high winds may lash the surface soil till it is gradually washed away in the places where it is not deep. Such occurrences are known, and possibly 1, 3, 4 and 7 are examples of this natural occurrence. In some parts of the west of Scotland this may occur on ground with a very slight slope.

On certain steep screes lichens do play two very important roles. First, they cover, or partly cover, the stones of the scree; and secondly, as fragments break off they help to form a medium on which algae and mosses may commence growth to be followed by grasses. Usually the closely attached crustaceous lichens appear first, followed by the foliaceous and/or shrubby type. It is about this stage that algae and/or moss protonema may appear. After the establishment of the foliaceous type of lichen, mosses begin to make appreciable progress in many parts of the scree. Then, with the establishment of mosses, grasses soon follow. Once this stage is reached and nothing occurs to upset the succession or destroy the vegetation, other plants may appear such as *Calluna vulgaris* and *Rumex acetosella*, which may appear much earlier than the grasses. Once most of the scree is clothed with these early pioneers quite a number of other plants may be found, such as *Galium saxatile* and others associated with a heathy vegetation. As the examples quoted show, the sequence is not always as outlined. Algae are not always found in any quantity. The early stages of colonization may be not mosses (Clements, 1916; Warming, 1909), but occasionally plants like *Teucrium Scorodonia*.

An interesting type of scree is that found by soil erosion after the destruction (by fire or otherwise), or the felling of a small wood or copse of trees on a hillside (Phot. 1). Here the succession will largely follow that already given, but in several screes examined liverworts have played a very important part. The liverworts concerned were *Ptilidium ciliare* and *Lophocolea bidentata*. On a

northern slope, one or both of these liverworts may quickly cover a large area of ground. When this occurs the succession is speeded up so that mosses do not necessarily play such an important part, but are largely replaced by grasses. *Lophozia Floerkii* also occurred, but it never played such an important role as *Ptilidium ciliare* and *Lophocolea bidentata*.

Screes which have a very steep slope often remain in a state of flux. This is due to the fact that wastage, always going on, is practically as great as—or greater than—any temporary gain in vegetation covering. This fluctuation may be seasonal or quite erratic, depending on weather conditions. Animals such as rabbits and sheep also disturb screes by making paths, burrowing and grazing such vegetation as may exist (Fenton, 1937*b*). Very often after heavy rain, melting snow or frost, there may be miniature landslides carrying down much debris and vegetation with them. Such screes might be described as being in a state of mobile equilibrium, and this may continue over an indefinite period, for example, no. 14.

It is perhaps worth mentioning that incipient screes are at times prevented, where all the soil is not completely eroded, e.g. after burning heather, a rapid covering of mosses may bind the remaining soil (Leach, 1931; Fenton, 1937*a*). The mosses which play an important part are *Webera nutans*, *Campylopus flexuosus* (bare peat), *Ceratodon purpureus* on heathy soil, *Hypnum cupressiforme* on peat, *Hylocomium squarrosum* on heathy soil and *Dicranium scoparium* of very general distribution. *Polytrichum commune* is sometimes very plentiful on damp and peaty soils and at times may form a closed community succeeding woodland. *Polytrichum juniperinum*, *P. piliferum* and *P. formosum* occur chiefly on dry heathy soils. At times many of these mosses may be found on screes. Several of the screes considered have much in common with heaths. In fact, the fluctuations in lichens, mosses and *Festuca ovina*, *Agrostis* spp., etc., often show remarkable similarity to what Watt (1938) has described for Breckland. The drought factor in spring, summer or autumn is probably an important one in determining the flora of many of the screes, except, perhaps, some with a northern aspect. The screes considered are quite different to the arctic-alpine type dealt with by Watson (1925) or even those dealt with by Evans (1932). There are resemblances, but owing to the drier climate near the east coast region, the conditions in many cases resemble more closely those of a heath (Watson, 1932).

The most outstanding characteristic of these screes is the very varied method of colonization. Where the stones or small rocks resist weathering lichens generally commence colonization. These are rapidly followed by *Rhacomitrium* spp., especially *R. lanuginosum*. Examples of this are nos. 1, 4 and 6. Where the surface disintegrates and small pieces break off and a soil of sorts is formed, lichens are not often frequent (Darbyshire, 1914), but certain mosses, grasses, and plants of the heath type prevail. In fact, the flora is similar to that of a heath and is quite different to that of erosion areas or

that of a true scree of higher altitude. No. 2 is a very early stage of this process and no. 10 of a later stage. It is of interest also to note that the mosses present were species of *Polytrichum* and not of *Rhacomitrium*. Where deeper rooted plants remain and where trees were formerly present there are generally some survivors of the woodland vegetation.

In these hill-grazing areas a large part of a scree may frequently be formed by stones and debris from a break at a higher elevation falling on and covering part of a hillside at a lower elevation, e.g. nos. 11 and 12. If this covering is not very deep it may not entirely submerge underlying vegetation and it may therefore early assume a rather curious appearance. For example, *Vaccinium myrtillus*, *Calluna vulgaris*, *Pteridium aquilinum*, certain ferns and *Polytrichum commune* and strong growing grasses may force a way through the surface cover of stones or bits of rock. It is very doubtful if such a formation should be called a scree—except in a very popular sense. Botanically it is much of the old vegetation growing through a covering of stones. If the area is not extensive it may be difficult to locate it after the lapse of some years. The scree already quoted from Cademuir is a good example of this type of formation, with vegetation coming through the surface covering of stones. The careful removal of the stones showed that soil was reached about a foot below the surface of the scree. In a comparatively short time such screes get covered with vegetation and in the later phase they closely resemble the surrounding vegetation. At a distance one such scree with a north-western aspect was a little difficult to detect. The vegetation of this scree was very similar to the rest of the hillside. The grasses were *Festuca ovina*, *Agrostis* spp. and a few plants of *Nardus stricta* and a little *Holcus lanatus* and *H. mollis*. The lichens were *Peltigera canina* and *Cladonia rangifera*. The mosses were *Dicranum scoparium*, *Hylocomium squarrosus*, *H. triquetrum* (a little), *Hypnum cupressiforme*, *H. Schreberi* and traces of *Rhacomitrium lanuginosum*. The other plants were *Viola lutea* and *V. canina*, *Luzula sylvestris*, *Campanula rotundifolia*, *Lotus corniculatus*, *Cerastium triviale*, *Polygala vulgaris*, *Thymus Serpyllum*, *Galium saxatile* and a little *G. verum*.

Another scree in progress of being clothed, particularly by invasion from the edges, gave the following vegetation: *Rhacomitrium lanuginosum* (plentiful), *Hypnum cupressiforme*, *Dicranum scoparium*, *Galium saxatile* (c.), *Festuca ovina*, *Agrostis* spp., *Deschampsia flexuosa*, *Nardus stricta* (o.), *Oxalis acetosella* (a little), *Vaccinium myrtillus* and one plant of *Cystopteris fragilis*.

Both these screes give, as it were, an intermediate phase between a typical scree and a heathy type of grassland, typical of the southern uplands of Scotland. There are, however, some very interesting features. The presence of *Cystopteris fragilis* was puzzling till a little examination showed that soil lay from six inches to a foot below the surface of the scree where the fern was growing. This led to a reinvestigation of the scree on Cademuir. After a little careful burrowing it was found that where *Mercurialis perennis* occurred the

depth of the scree varied from nine inches to a foot in depth, and that the plants were rooted in the soil below and growing through the scree. This was also true of *Oxalis acetosella* and *Teucrium Scorodonia* in another part of the scree where careful examination revealed soil below. Hence it is evident that some at least of the plant cover consists of the original vegetation. The presence of *Hylocomium triquetrum*, as pointed out elsewhere (Fenton, 1937a), indicates the site of former woodland. This is borne out by the presence of *Digitalis purpurea*, *Oxalis Acetosella*, *Mercurialis perennis* and some fragments of birch found buried in the scree. It suggests that many of these screes arose shortly after the destruction of a birch copse or wood, or a mixed wood, which led to soil erosion and movement of stones and rocks downhill. This has undoubtedly occurred in the past and may still occur after the felling of a wood on a steep slope on thin soil. Even at the present time, in several places, remains of the wood or copse, with bare stones or rock on the site, afford good supporting evidence.

It is quite impossible to estimate the stability of the screes quoted. No. 14 will always remain unstable as the slope is very steep. The other examples should one day be covered with vegetation, although it may in some examples (no. 11, Cademuir) take a very long time. The chief disturbing influence is grazing animals, rabbits and sheep (Fenton, 1937b). Apart from grazing, burrowing and scraping cause much erosion. If a large area could be successfully fenced—and maintained—against animal (and human) interference, there is no doubt that colonization would tend to proceed much more rapidly. Scree no. 10, which has for years been extending, is only now very slowly but gradually becoming colonized. As far as one dare estimate it will be several generations (provided there is no destructive force at work) before it ceases to be a scree. The other examples are all in various stages of being colonized.

It is exceedingly difficult to determine in many cases whether the vegetation represents primary colonization or retrogression, or if both of them are operating. Changes are slow and the past history usually unknown. Interference by animals also tends at times to upset the vegetation. Briefly, nos. 1, 2, 3, 4, 6, 7 and 10 have reached their present stage by primary colonization. Nos. 5 and 9 are doubtful. Nos. 8, 11, 12 and 13 are examples of retrogression with colonization occurring in places.

No conclusive evidence could be obtained that solifluction had played any part in scree formation (Hollingsworth, 1934).

SUMMARY

The origin and structure of screes in the Pentland and the northern part of the Moorfoot Hills is described.

The flora is given of typical examples.

Compared with screes in the Lake District, Merionethshire, and those of arctic-alpine type, the flora is much more restricted.

The colonization of bare screes is discussed. There is a considerable difference in the pioneer types.

Lichens, algae or mosses, may be the pioneers. In some cases there is a distinct series of phases: lichens, algae, moss, grasses, followed by dicotyledons.

Where screes have developed, due to erosion after the felling or destruction of trees, liverworts (e.g. *Ptilidium ciliare*, *Lophocolea bidentata*) sometimes play an important part in covering the scree.

Where scree debris covers existing vegetation, certain plants may succeed in pushing up through the stones or small pieces of rock, so that a vegetation cover, or partial cover, may develop very quickly. There is some evidence that the screes showing this formation are due to erosion following the cutting or destruction of wood.

Where rapid surface disintegration of stones and rock occur, a sandy "soil" may form with a flora typical of a heath.

REFERENCES

- Clements, F. E. "Plant succession." *Publ. Carneg. Instn.*, 1916.
- Crampton, C. B. "The vegetation of Caithness considered in relation to the geology." *Comm. Surv. Study Brit. Veg.* 1911.
- Darbyshire, O. V. "Some remarks on the ecology of lichens." *This JOURN.* **11**, 71-82, 1914.
- Evans, E. Price. "Cader Idris. A study of certain plant communities in South-west Merionethshire." *This JOURN.* **20**, 1, 1932.
- Fenton, E. Wyllie. "The vegetation of an upland area (Boghall Glen, Midlothian)." *Scot. Geogr. Mag.* **49**, 332, 1933.
- Fenton, E. Wyllie. "The value of certain mosses in detecting old woodland sites." *Fourth Int. Grassl. Congr., Aberystwyth*, pp. 159-63, 1937a.
- Fenton, E. Wyllie. "The influence of sheep on the vegetation of hill grazing in Scotland." *This JOURN.* **25**, 424, 1937b.
- Hollingsworth, S. E. "Some solifluction phenomena in the northern part of the Lake District." *Proc. Geol. Ass.* **45**, ii, 167, 1934.
- Leach, W. "A preliminary account of the vegetation of some non-calcareous British screes (Gerolle)." *This JOURN.* **17**, 321, 1930.
- Leach, W. "The importance of some mosses as pioneers on unstable soil." *This JOURN.* **19**, 98, 1931.
- Wallace, R. *Heather and Moor Burning for Grouse and Sheep*. Edinburgh, 1917.
- Watson, W. "The bryophytes and lichens of arctic-alpine vegetation." *This JOURN.* **13**, 1, 1925.
- Watson, W. "The bryophytes and lichens of moorlands." *This JOURN.* **20**, 284, 1932.
- Warming, E. *Oecology of Plants*. Oxford, 1909.
- Watt, A. S. "Studies in the ecology of Breckland. III." *This JOURN.* **26**, 1, 1938.

BRITISH ECOLOGY DURING THE PAST QUARTER-CENTURY: THE PLANT COMMUNITY AND THE ECOSYSTEM

By A. G. TANSLEY¹

FIRST of all I must express my lively sense of the great honour the Society has done me by electing me to its Presidency for a second time. It is an interesting and on the whole a cheering exercise to look back over the quarter-century that has elapsed since the foundation of the Society, to compare my estimate of the position of British ecology in 1914 with what we may say of it to-day, to contemplate the good work that has been done during the period, and the promise of the future.

Nearly all that I said of ecology as a subject in my Presidential Address of May, 1914, on the eve of the Great War, is still, in my judgment, true. The ecological outlook on biology is vitally important, not only to pure science but because of its application to human life and activity in the widest sense. The difficulties of the subject are still very much what they were 25 years ago, and the right ways to overcome them have not changed. In 1914 I looked forward confidently to a development of ecology which would give it a much higher status in the estimation of biologists at large and of those who should be concerned with its practical applications; and this expectation has been to a large extent realized. It is true that progress has been somewhat slower than I anticipated—at least in my more optimistic moments. But what we may call the rise in ecological stock has been fairly proportional to the increase in value and interest of the work produced—and that is as it should be.

I think it is still not clearly enough realized, especially by those biologists who are not ecologists, that ecology is not so much a special branch of biology—in the sense that genetics or the physiology of nutrition are special branches—as a way of regarding animal and plant life. Its development depends on the application of various kinds of biological technique, as well as the techniques of physics and chemistry, to the problems presented by animals and plants studied in their natural and semi-natural environments. To these borrowed and adapted techniques are added those of the ecologist's own devising.

A large part of the future work of plant ecology will, I think, be concerned with life form and its relation on the one hand to environment and on the other to heredity. Necessarily involved in this work is the whole problem of the phenotypic complexes which we call species and their relation to genetic constitution—a topic recently brought prominently to the attention of the

¹ The President's Address at the adjourned Annual Meeting of the British Ecological Society on the 4th of April 1939.

Society, and one which *primarily* concerns geneticists and taxonomists rather than ecologists. Again when we think of the fundamental determination of vegetation by soil and climate we realize that the methods and results of pedology and climatology, including micro-climatology—a subject as yet very little developed—are of first importance to the ecologist. Certain parts of plant physiology have always been recognized as ecologically fundamental—the effects of temperature, the whole of the plant's water relations, and the effects of different ions in the soil solution and of the oxygen and CO₂ content of the soil atmosphere on soil organisms and on absorbing roots, the effects of different intensities and qualities of illumination.

Thus the plant ecologist must constantly concern himself with the methods and results of investigators both in different branches of botany and in other sciences. These he uses for his own purposes, focusing them, so to speak, on his proper study of individual plants, ecotypes or species in their natural homes, and of the aggregates of individuals that we call plant communities.

THE PLANT COMMUNITY AND THE ECOSYSTEM

The specific contribution of plant ecology as an independent discipline is of course the concept of the plant community, with the series of supplementary concepts based on the attempts to classify communities and on the facts of succession. The community concept can be transferred to animals only to a limited extent and attempts have been made to construct concepts—such as the “food chain” and the “pyramid of numbers”, “environmental resistance”, “biotic potential”, and so on, which shall bring together some of the characteristic phenomena of interdependent animal life. How far these will play a part in the development of ecological theory the future will show. Since animals depend upon plants, directly or indirectly, for their food and often for indispensable shelter, and since vegetation is affected by animals in varied and far-reaching ways and some species of plants depend upon animals for their maintenance, it is clear that animal and plant populations inhabiting the same unit of space are very closely knit together. For this reason a wider concept has been formulated, the *biome* or *biocoenosis* (which some have called “the biotic community”), applying to animals and plants taken together. I myself have preferred a wider concept still, the *ecosystem*, which includes the inorganic as well as the living components in the whole to be considered.

The universe may be regarded as consisting of a vast number of physical systems of all sorts and sizes, whose only common character is that each shows a certain autonomy in its organization and tends towards a condition of equilibrium represented by its characteristic mature structure. This concept of the physical system is not affected by changing views of the nature of matter and energy. Physical systems may be divided¹ into two categories—

¹ Lewis, *A System of Physical Chemistry*.

those which are and those which are not in equilibrium, and in the plant community, or the ecosystem of which it forms part, the distinction corresponds with the difference between a climax and a seral community, a mature and an immature ecosystem. We must remember, however, that the changes in a system may be very slow, so that it may appear to have attained equilibrium when it has not really done so, but only presents an apparent or "false" equilibrium. It would, I suppose, be possible to contend that the apparent equilibrium of every climax community is a false equilibrium, that slow changes are always taking place which will ultimately destroy it or change it into something else. But here, I think, the ecologist is justified in giving weight to the time factor, in adopting the concept of *relative equilibrium* to apply to systems in which the changes are so slow that the system does not lose its essential character (except as a result of the changed incidence of external factors) within any period of which we can take cognisance.

Physical systems range from the universe itself, which is certainly not in equilibrium, though it is completely autonomous since by hypothesis it is all-embracing, down to the atom with its planetary organization of electrons, probably representing the most perfect and stable dynamic equilibrium known to science. Between these extremes come a multitude of intermediate systems, the larger including a vast number of the smaller, overlapping and intersecting one another in space in the most various ways. Some show considerable autonomy and stability, resisting disturbance and maintaining at least an approach to dynamic equilibrium for a long time. Others are continually being destroyed and reconstructed, in the same or in modified forms, while others again are so unstable and imperfect in organization that it is hardly legitimate to consider them as systems at all. None—not even the atom—is immune from interference and disintegration. Both the universe at large and that minute portion of it represented by the surface of our own planet, are littered, so to speak, with the wrecks of systems that have been destroyed; but everywhere we see the tendency to fresh organization, to the initiation of new systems, to the re-establishment of old types of equilibrium or the establishment of new ones.

An individual living organism represents a type of system that is highly characteristic and indeed unique. Each is extremely complex and very highly integrated, and each maintains what seems to be a wonderfully perfect dynamic equilibrium for a certain period; but all—at any rate all that have a differentiated soma—contain the seeds of their own decay and are thus examples of the physicist's "false equilibrium". What I have called an ecosystem is far less integrated than an individual animal or plant, but it shows itself capable, nevertheless, of a certain degree of integration, of a certain resistance to disintegrating forces, and thus of maintaining, in certain cases, a *relative* dynamic equilibrium for centuries or even for millennia. We

do not know enough to say whether the equilibrium of an ecosystem is always false, but it is certain that its plants and animals, together with all the inorganic factors on which they depend, work together to create a balanced structure which is self-maintaining, and that is the essential characteristic of a physical system.

We usually call the part of the system composed of plants a *plant community*, and the usefulness of this conception is far from exhausted, because the plants of which it is composed live together gregariously in a certain harmony, and such an aggregation of plants, for example in a natural forest, is in a very real sense the kernel of an ecosystem. Within a complex plant community such as a tropical rain forest, or a self-regenerating European deciduous forest, even within much less complex communities such as grassland or fen, a number of minor communities can be distinguished—"synusiae" as Rübel and Gams called them many years ago—and these may themselves show a considerable degree of autonomy. Synusiae are much more homogeneous than the complex plant community of which they form parts, their members often having a common life form, and they were regarded by Gams as the most fundamental units of vegetation. They commonly characterize a particular stratum or layer of the vegetation, and the lower strata of a forest whose dominants cast deep shade depend for their existence on the moist air and soil and sometimes on the weak light of their partial habitat. Under less protected conditions they may be largely or wholly independent of the forest dominants, so that lower stratum synusiae may exist under various trees which cast but little shade or even in the complete absence of trees. This is conspicuously true of many northern heath, moss and lichen communities, which may be associated with open oak, birch or pine wood, or may exist on open "heath" without any trees. It is also true of the so-called savannas and savanna forests of south-central Africa, where the same grasses may be dominant in the field layer of forest casting light shade, and also in the absence of trees.

The relative independence, and sometimes the complete independence of such stratum communities, has led Lipmaa to assert recently that the "one-layered community" is *the* fundamental unit of vegetation, and Du Rietz has proposed what seems to me the unnecessary name of "union" for such a layer or stratum community—a proposal which was accepted (as I think unfortunately) by the Amsterdam Congress in 1935. The term "synusia" for communities of homogeneous or relatively homogeneous life form living under narrowly defined conditions of life is very useful, and when such communities characterize different strata of a larger stratified community "stratum (or layer) synusia" seems quite adequate and more immediately intelligible. These stratum synusiae must always be studied separately, however closely they may be dependent on other strata of the larger community to which they belong, for since each lives in a well-defined "partial habitat", each has a structure and economy of its own. Furthermore the shrub and field layers

of deciduous summer forest, for example, are to a certain extent independent of the *particular* dominants of the tree layer. But so far as there is actual dependence of one layer upon another the layer *synusiae* must be treated as parts of a more or less integrated whole, as constituents of an ecosystem. Of course there are very different degrees of integration, and when the layer *synusiae* are really functionally independent of one another's presence there is no integration at all. The *synusiae* present are then held together, so to speak, only by their common dependence on the same climate and soil, and really form separate ecosystems.

At the other extreme from Lipmaa's overemphasis of the "union" or dependent *synusia*, we have the attempt to replace the conception of the plant community by that of the "biotic community". I dislike the term "biotic community". Animals and plants are too radically different in their modes of life to be usefully considered as "members" of one "community". The fundamental correspondences between them depending on the unity of living substance are far more physiological than ecological. Ecologically plants and animals are primarily antagonistic. The same is to a large extent true of green plants and fungi, and if we are to consider fungi as plants, we are here faced with the limitations of the concept of community. Green plants, fungi and animals, including soil bacteria and soil animals, are all parts of the ecosystem, but so are the inorganic components. When we want to speak of all the living organisms of an ecosystem together, the term *biome* is terse, convenient, and carries no misleading implications. The impulse to replace "plant community" by "biotic community" is due of course to enhanced realization that it is quite unscientific to ignore or minimize the role of the animals in the ecology of a plant community. Together with the inorganic factors they are elements of the environment of a plant community; while the plants and the inorganic factors are parts of the environment of an animal community where we can properly speak of an animal community. But we cannot escape from the primacy of the green plants, which are the foundation of all life, and it is because of the fact that green plants live together and make the same *general* demands on their environment, as well as because they are often interdependent, that the conception of a plant community remains useful. Methodologically it is usually necessary to study the green plant aggregation and the animal aggregation separately. Often it is necessary to split up each of these into separate smaller aggregations—such as the *synusiae* of which I have spoken—that make different demands on their environment, while the members of each make approximately the same demands. The only natural synthesis of the whole is the ecosystem, of which all these, together with the inorganic factors—the climatic and soil complexes—form part.

Before leaving these general considerations I may devote a word or two to the demand that we should consider the biome as an *organism*, just as Clements formerly insisted that the plant community should be considered

as an organism. It is true that any aggregate of plants and animals living together may develop some of the characteristics of an individual organism, and the more integrated such an aggregate becomes the closer its resemblance to a single animal or plant. I myself have gone so far as to call such aggregates "quasi-organisms". But it is obvious enough that the correspondence is far from exact, and the radical differences are not removed by calling the community or the biome a "complex organism". We can, if we like, call the *ecosystem* an organism because it shows organization, just as some philosophers, for example Whitehead, call the universe an organism. But most biologists will prefer to restrict the term, as they have been accustomed to do, to the individual animal or plant. In this sense the word may fairly claim to have become a well-established biological technical term.

It may seem a far cry from this essay in the theory of ecology to the daily work of the ecologist, but I do think it useful and even important that the working ecologist should sometimes consider what it is that he is really investigating. The ultimate object of the synecologist's study, as I see it, is the ecosystem—its structure and working; its origin and fate; the factors and mechanism of its development and maintenance; the forces which maintain its stability or threaten it with disintegration or destruction. By keeping these objects constantly in mind the student or investigator will orientate his work in relation to fundamentals even when he has to spend most of his time in the description of surface phenomena. I have always tried to impress on my students, perhaps sometimes *ad nauseam*, the essential importance of the study of succession, and this mainly because succession consists in the changes involved in the development, modification or destruction of the ecosystem, its progress towards the equilibrium represented by so-called climatic, or some other kind of climax, or its disturbance by and reaction to allogenic factors, resulting in progress towards some fresh position of equilibrium when the allogenic factor is constant in its operation. The establishment of the facts of succession, the series of plant populations that appear in a given habitat is a necessary preliminary, but we should always try to investigate how and why those particular plant populations appear and displace one another—the mechanism of their competition as it is conditioned by the changing habitat, and the consequent progress towards the equilibrium of the ecosystem.

THE BRECKLAND

The outstanding pieces of synecological work that have been published in this country during the last 25 years will illustrate what I mean. First there was Farrow's work on the Breckland, mainly carried out between 1913 and 1917. In this he showed that on Cavenham Heath the constant and overwhelming pressure of rabbit grazing was the effective factor which converted Callunetum into *Agrostis-Festuca* grassland, demonstrating by means of experimental exclosures that Callunetum, which could not maintain itself

under the rabbit pressure, whereas the grasses could, regenerated from eaten down stocks of *Calluna* in the closely nibbled grassland when rabbits were excluded, and could then re-acquire dominance. He traced the differential effects of rabbits on various species to differences of palatability which led to some suffering more than others and thus being placed at a disadvantage in competition. In this way there arises a local zonation of different dominants round points or areas or along belts of maximum rabbit pressure. A species which is severely eaten may nevertheless gain an advantage in competition with another which is more severely eaten, or whose life form and mode of growth makes it less able to maintain itself under rabbit attack. He also showed that comparable phenomena were widespread in other parts of Breckland and in regions outside its limits. Farrow did not confine his investigations to the effect of the rabbit factor, but also studied experimentally the results of increased water supply on the growth of different species, as well as the effects of blowing sand and the reactions of the vegetation. Everywhere he concentrated on the dynamic factors which changed the vegetation, and thus made a notable contribution not only to ecological knowledge but to the method of attack on ecological problems. By so doing he carried widespread conviction and gave the best lead for future work on similar lines. While the decisive influence of grazing in altering vegetation was of course generally recognized, this was the first systematic and experimental research into the details of a particular case—the destruction of one plant community, the Callunetum, and its replacement by another as a result of the incidence of a new factor.

THE HYDROSERES

Then came Pearsall's work on the vegetation of the English Lakes and their associated marshes, fens and bogs, begun in 1914 and continued at intervals for many years. Here the investigator was dealing with the multiform hydrosere of fresh water under a definite range of conditions. Pearsall identified and described the submerged, reedswamp and fen communities present, and traced the sequences from one to another. He was able to distinguish two main trends of succession depending respectively on the presence or absence of silting by inorganic material relatively rich in basic ions. With abundant inorganic silting *Nitella*, *Najas flexilis*, and linear-leaved pondweeds occurred in deep water, in the shallower *Littorella uniflora* and *Nymphaea alba*, followed by *Scirpus-Phragmites* reedswamp, with *Typha latifolia* on the richest silts. On the poorest inorganic soils (stony lake bottoms) *Isoetes* was a pioneer, followed, as submerged peat accumulated, by *Juncus fluitans* and *Potamogeton natans*. In shallow water *Lobelia dortmanna* corresponded with *Littorella* in the other type of sere, and the dominants of the reedswamp were *Equisetum fluviatile* and species of *Carex* such as *C. inflata* and *C. elata*. There were however constant changes from one of these trends to the other, depending on the incidence or cessation of inorganic silting, so that the actual seres observed

were very various. In the absence or after the stoppage of silting acid peat always accumulated.

With the rise of the soil surface above the water level a corresponding contrast was apparent. Richly silted areas, frequently flooded by a beck carrying a load of inorganic silt, developed fen dominated by *Phalaris* and *Calamagrostis*. This was colonized by *Salix purpurea* and *S. decipiens*, and to some extent by alders. It seemed probable, though the succession could not be clearly traced, that alder and birchwood might develop here as on the East Anglian fens, but it is unlikely that the climax sessile oakwood of the Lake District hillsides would appear, except on well-drained gravelly soils. On areas of slower sedimentation *Salix atrocinerea* was the only shrub colonist, and here the salallows formed closed carr, which however showed no sign of regeneration and is probably quite transitory. Finally, where silting is very slow or in abeyance, *Molinia* with *Myrica gale* invades and displaces the Phragmitetum or Caricetum. The Molinietum is but sparsely colonized by woody plants, and *Sphagnum* is present, apparently forming the starting-point of raised bog development.

Thus in this Cumbrian climate, intermediate between the more continental conditions of East Anglia and the extremely oceanic climate of western Ireland and western Scotland, edaphic differences were shown to be sufficient to switch the succession towards a forest or towards a bog climax. Climatic conditions similar to those of Cumbria probably hold in north-east Ireland, where, according to White's observations, *Salix* carr is poorly developed and bog or "moor" succeeds the fen. In the East Anglian climate, on the other hand, reedswamp or fen is normally succeeded by forest—alder and birchwood certainly, and probably oakwood. Locally Sphagneta and their characteristic associates occur, but there is no evidence that raised bog is now being formed in this region—though it certainly was at one time, for several feet of *Sphagnum* bog peat have been found in the Woodwalton fen area, and there is said to be good evidence that an oxyphilous flora was widespread in the Fenland in quite recent times.

There are several problems connected with the East Anglian hydroseres that are not by any means satisfactorily solved. The status of fen itself is not completely clear. For the formation of fen peat a good supply of basic ions, usually Ca, seems essential. But the considerable areas of fen that exist in east Norfolk, and the small fragments left in the Fenland proper are certainly maintained by mowing. When mowing ceases the fen is at once occupied by carr. Some people contend that fen is always an anthropogenic vegetation and that under completely natural conditions carr would always follow directly upon reedswamp or upon the parallel tussock swamp. But this view is apparently contradicted by the great areas of prehistoric fen peat, several metres in thickness, that commonly underlie raised bog—unless indeed we regard this so-called fen peat as really reedswamp peat. Reedswamp is not

of course sharply delimited from fen, the line between them being drawn where the growing peat reached the water level, i.e. the *summer* water level; and many of the same species, e.g. *Phragmites*, *Cladium* and some Carices, occur in both. Godwin has shown that the level of bush colonization of the fen at Wicken corresponds with, and is presumably determined by, the *winter* water level, and it is very likely that the extent of "natural" fen depends upon the depth of winter flooding. Where this is great the vertical distance between the summer and winter water level is increased and will determine a correspondingly greater horizontal extent of fen between the upper limit of reedswamp (summer water level) and the lower limit of carr (winter water level). The deep winter flooding of the Lough Neagh fens may in fact be the cause of their great extent.

I have devoted some little time to the hydroseres because they illustrate not only the kind of knowledge that has already been obtained as the result of Pallis's excellent pioneer work on the Norfolk Broads (carried out before the 25-year period I am considering) and Pearsall's admirably thorough and illuminating study of the Cumbrian Lakes, supplemented by the more recent researches of White on the Co. Armagh fens and of Godwin and his collaborators mainly on Wicken Fen; but also because the work that has been done illustrates the lines that must be followed in solving the problems which remain. What is wanted now is a thorough re-investigation of the east Norfolk hydroseres on the lines of Pearsall's work, from the submerged communities right up to the establishment of oakwood, together with a comprehensive study of the varied alluvial soils—the peats and the various organic and inorganic silts, their stratigraphy, and the conditions of their formation. Taken together the hydroseres form a complete and complex prisere, our knowledge of which is already greater than that of any other prisere in the British Isles. The interest centres in the continuous and mainly autogenic change from one community to another throughout the series—a continuous progress towards a condition of equilibrium represented by some type of woodland, or in the western climates by bog or moss. But in the arrest of the sere in the stage of fen by repeated cutting we have the establishment of a new ecosystem, what I have called a *plagioclimax*, following the suggestions of Godwin on what he called *deflected succession*. Godwin pointed out that when a prisere is interrupted by some external factor such as the mowing or grazing of a seral stage, succession is not immediately stopped in a "subclimax" according to the original conception, but continues on a new course, from which it rejoins the original course of the prisere if the interrupting and deflecting factor is removed. This "deflected succession" Godwin illustrated by the phenomena at Wicken Fen, where frequent cutting of *Cladium*, the fen pioneer, does not lead to the stabilization of Cladietum but to the appearance of *Molinia* and the transformation of Cladietum into Cladio-Molinietum and eventually pure Molinietum. When mowing is stopped bushes colonize any

one of these three communities, and carr—the next stage of the prisere—develops. Molinietum does not here appear to form any part of the prisere itself.

CHALK GRASSLAND

With this we may compare the xerosere on chalk soil. If the mixed herbage developing on a bare chalk substratum is grazed, woody plants are prevented from colonizing it and the normal succession to scrub and woodland is interrupted. Continued grazing leads to the formation of typical chalk pasture, often *Festucetum ovinae*, with its characteristic assemblage of grasses and herbs. All or most of its members may be present in the ungrazed herbage, including *Festuca ovina* in abundance, but the grazing *Festucetum* is not a stage of the prisere, it is created by the continuous grazing, just as the fen Molinietum is created by continuous and frequent mowing. The course of events leading to the grazing *Festucetum* has not been so precisely determined as that which leads to the mowing Molinietum, but there is enough evidence to suggest that the cases are parallel, and that the grazing *Festucetum* may fairly be called a plagioclimax, stabilized by the grazing factor, and remaining essentially the same thing so long as sheep grazing continues. We do not of course know that the *Festuceta* of our chalk downs are not themselves slowly changing, nor can we positively assert the absence of slow continuous change in any climax whatever. In the presence of a constant external factor we should however expect an approximation of the ecosystem to equilibrium. The equilibrium may be "false" in the physicist's sense, but I think it is valid for the ecologist.

BRITISH BEECHWOODS

Another outstanding synecological research is A. S. Watt's work on the British beechwoods. Beginning in 1914 with a systematic study of the causes of the wholesale disappearance of acorns and oak seedlings in our oakwoods, Watt extended this work, after the interruption of the war, to beechmast and beech seedlings. From this he was led to a general study of the structure and development of beech communities. Working at first on the beechwoods of the western South Downs, he afterwards extended his field to the Chilterns and to the subsponaneous beechwoods of Aberdeenshire. Watt dealt with three types of climax beechwood, on rendzina, brown earth, and podsol respectively, the last being very likely a "pseudo-climax" in the sense that it is not stable. So far as material was available he worked out the later phases of the seres leading to the beech consociations from the stage of grazed grassland (or heath). On the rendzinas and brown earths the grasslands are the necessary starting-points, because so far as it is not arable and is not occupied by one or other of the woody communities representing the later stages of the seres, all this land in the southern beech region has been used for grazing. On the rendzinas (shallow soils of the chalk escarpments and valley sides) Watt recognized a chalk scrub stage primarily dominated by

hawthorn or juniper, an ashwood stage, and finally the climax beechwood. In the less maritime climate of the Chilterns, and particularly in exposed situations, the ashwood stage is missing, beech directly colonizing the scrub. On the brown earths (loams) scrub of gorse or hawthorn with a much smaller representation of the calcicolous shrubs is colonized by ash and oak, giving rise to an ash-oakwood as preclimax to the final beechwood. The dominance of ash or oak in this preclimax stage seems to correspond directly with the calcareousness of the soil (or with some correlated factor). On the more calcareous soils ash is most conspicuous, on the less calcareous oak. On the heavier clay soils oak has an advantage over beech and the climax may be oakwood. But the natural phenomena are here much obscured by the type of exploitation. On the pod sols the succession has not been so closely worked out. The normal succession on the sand and gravel pod sols of the south of England seems to be Callunetum → birchwood → oakwood → beechwood, with subspontaneous pinewood often developing in the intermediate stages. The beechwood which appears locally on these soils is in Watt's opinion unable to maintain itself for more than one generation owing to the accumulation of a compact surface layer of dry peat or "mor" from the beech leaf litter and accompanying mosses, tending to prevent the germination of beechmast and the establishment of seedlings. On the Aberdeenshire pod sols Watt regards subspontaneous beechwood as a "post-climax", also unable to maintain itself in a climate whose natural climax vegetation is, he thinks, "pine heath".

In these seres leading to beechwood, then, we have the establishment of mature self-maintaining climax communities or ecosystems on the rendzinas and the brown earths, while on the less favourable pod sols the highest type of community is apparently not stable, so that we may perhaps have a cyclical development—heath → beechwood, beechwood → heath. If it should be established that this process is real and automatic the whole cycle would represent a more complex kind of ecosystem in which the conception of development to a stable climax has no place. It may be that such cyclical systems have a much wider application to vegetation than we suspect at present. At a lower stage of the succession, on the non-podsol soils, the grazing factor diverts the sere into the plagioclimax of chalk pasture on the rendzinas, and a somewhat different type of pasture on the brown earths. I have already given reasons for holding provisionally that mature chalk pasture is itself an ecosystem in relative equilibrium.

We are all looking forward, I am sure, to the completion of Dr Watt's researches on Breckland vegetation upon which he has now been engaged for several years, and of which three instalments have been published. It will be of great interest to see whether any positions of equilibrium, other than rabbit grazed *Agrostis-Festuca* grassland, can be established in this region, subject, as it is, to conditions of climate and soil which are in some respects extreme within the British Isles. The first requisite is a far more extensive and accurate knowledge of the facts, as Watt has clearly realized.

AUTECOLOGY

In the foregoing discussion I have tried to focus the more significant synecological work of the past quarter-century under a single point of view, and to show that the ecosystem is the most fundamental synecological concept to which our enquiries into vegetational phenomena and processes can be related. In trying to estimate the progress that has been made during the last 25 years we must not however forget the numerous studies which do not deal with whole plant communities or with succession as such, but with the autecology of particular species or with other ecological problems.

It has become a commonplace in ecological circles that in order to understand the communities themselves we want much more knowledge of the autecology of the dominants, the conditions under which dominance is established, and the behaviour of dominant species in competition within their geographical range but outside their range of dominance. The first requisite is a thorough knowledge of the morphology and life history of the species. Notable contributions in this direction have been made by the Rev. T. A. Jefferies for *Molinia*, by the late Dr Mukerji for *Mercurialis perennis*, and more recently by Miss Verona Conway for *Cladium*. Quite lately too Dr Watt has been investigating the morphology and mode of growth of *Pteridium* in the Breckland. The more we have of such studies and the more thorough they are the better position we shall be in to estimate the roles of the dominants in competition with other species. In addition to field observations and experiments, which are of course indispensable, we need carefully thought-out experiments on the species in culture, to determine as far as possible their requirements and behaviour in the absence of competition. Studies of what I may call "controlled competition", such as those tentative experiments with two species of *Galium* for which I was responsible more than 20 years ago, also throw much light on the competitive behaviour of species in their natural habitats.

Then there is the separation and study of strains of different growth form, which may also be ecotypes within an aggregate species. Much of this work has been done by Sir Reginald Stapledon's staff at Aberystwyth on pasture grasses and clovers. It cannot of course be separated from the finer taxonomy and the genetics of the various strains which make up an aggregate species; and in this field Dr Turrill and Mr Marsden Jones have done and are doing notable work at Kew and Potterne. What I think is of supreme importance here is much closer co-operation or union between taxonomists and geneticists on the one side and ecologists on the other. It is a very great pity that there is not at least one professed ecologist of ability and imagination attached to the Aberystwyth staff. A great number of ecological problems are constantly arising in the pasture work there, and the fully occupied staff cannot be expected to pursue them as they should be pursued. A young post-graduate

with ecological training could hardly do better than attach himself to the school and take up some of these problems. I am sure he would find a warm welcome and every help and encouragement. Sir Reginald himself is at heart an ecologist though he is obliged to occupy his time with many other matters.

STATISTICAL ANALYSIS OF DISTRIBUTION

The quantitative distribution of the individuals of a species within a given small uniform sample of a community is a valuable datum, which, in a pioneer or early seral community, throws light on the method of colonization, and in a mature community is presumably the resultant of two factors—the original mode of colonization and competition with other species. Statistical analysis of such data, which has been undertaken by Mr Geoffrey Blackman, Dr Clapham, and in India Dr Singh (among others), gives a measure of the approximation of distribution to true “random” dispersion and of the degree of “over-” or “under-dispersion”, i.e. of local aggregation or a tendency to equal spacing. But to gain *ecological* knowledge statistical analysis of the nature of distribution of a species must be accompanied by a study of its autecology—of its seed dispersal, vegetative propagation and power of competition, so that we can get an insight into the causes of the observed distributions.

PEDOLOGY AND EDAPHIC FACTORS

Progress in our understanding of edaphic factors has been considerably assisted by the great advances of pedology or soil science during the last 25 years.

The broad classification of our soil types into the “world groups” of brown earths, podsoles and rendzinas, with meadow (alluvial) soils and the two main kinds of peat—fen peat and bog or moor peat—though it is far from exhausting what we need to know about a given soil, does provide a good framework corresponding well enough with the broad features of the vegetation. Of more specifically ecological studies on soils, Mr De Silva, one of Prof. Salisbury’s pupils, has contributed a very useful paper on the distribution of certain species in relation to exchangeable calcium. There is no doubt that exchangeable calcium, and to a less extent other exchangeable bases such as potassium and magnesium, is one of the essential factors in the making of a “good” soil, and the amounts of these available bases, which is at least equally important with pH value, is now beginning to receive the attention it deserves. Decidedly acid soils, such as some of the clay-with-flints covering the Chiltern plateau, with pH values lying mainly between 4 and 5—though the subsoil may be as high as 6—with good mild humus, and relatively rich in exchangeable calcium, bear luxuriant vegetation of “exacting” plants. The soil reaction is an extremely useful ecological datum and often of crucial value, but it has to be considered along with other important soil characters. In this connexion Pearsall’s recent

papers on the "oxidation-reduction potential" of a number of different natural soils bearing characteristic vegetation are of great interest. It is of course a commonplace that the roots of ordinary mesophytes require a good supply of oxygen for respiration and the same is true of soil animals. A "fertile" soil is always a well-aerated soil. Pearsall has shown that very acid but relatively dry "mor" soils such as occur in woodlands with *Vaccinium myrtillus* and *Deschampsia flexuosa*, on *Calluna* heath and in drying *Sphagnum* bogs, are freely oxidizing though they do not produce nitrates, which begin to appear only when the pH value is above 3.8; while wet soils, though their pH value is above this point, are reducing, and also do not produce nitrates owing to the deficiency of oxygen. The broad distinction between "mull" and "mor" soils and their vegetation has been well known since P. E. Muller's work in the last century. The fertile "mull" soils, whose natural vegetation includes exacting species, are well aerated, have a high base status and are freely nitrifying, but as we have seen they may be decidedly, though they are never extremely, acid. The "mor" soils which bear only specialized oxyphilous vegetation may also be oxidizing, but they are deficient in bases, do not produce nitrates and are always extremely acid. Fungi are the dominant non-chlorophyllous plants. "Mull", according to Romell, represents a system in delicate dynamic equilibrium, in which the abundant soil animals keep the fungi down, and aerobic bacteria, including nitrifying bacteria, are dominant. The part of the ecosystem represented by green plants consists of broad-leaved trees and luxuriant exacting herbs, which absorb the basic ions and nitrates very freely, returning them to the soil in their leaf litter and other organic debris, so that there is a constant turnover of mild humus, abundant supply and rapid decay of organic material.

"Mor" on the other hand represents a very different system in which bases are deficient and fungi predominate, the organic material is not rapidly decomposed and tends to accumulate indefinitely, forming wet or dry acid peat. Fen peat represents quite a different system and requires further investigation. Clearly it has essential points in common with those marsh soils which bear similar luxuriant helophytic vegetation.

CLIMATE AND VEGETATION

The study of the effects of climate upon vegetation is in an unsatisfactory state. Certain broad correlations are very well known and indeed sufficiently obvious, but anything like a quantitative basis is almost entirely lacking, and we are often reduced to speculative and rather unconvincing conjecture or to a blank confession of ignorance. The subject is in fact full of difficulties—not only the frequent dearth or inapplicability of meteorological data, but the extreme complexity of the relations between climate, soil and vegetation. One example of this is the problem of so-called "compensating factors". A conspicuous case is the existence on dry well-drained soils in a very wet

climate of vegetation characteristic of damper soils in a drier climate, and vice versa. There has been no serious attempt to measure and compare the effects of climatic and edaphic water supply.

The subject of microclimates has been too largely neglected by plant ecologists. Almost the only data that have been collected are records of air humidity and light in the different layers of stratified communities such as woodland and very little use has been made of them. Entomologists on the other hand have recently made some remarkably interesting studies of the microclimates inhabited by definite communities of insects. I am sure that a great deal can be done by the plant ecologist in the close investigation of microclimates and their effect on vegetation, and that significant, perhaps surprising, results would be obtained.

PHYSIOLOGY OF VEGETATION

I cannot now discuss the rather disconnected studies that have been made from time to time of what may be called the physiology of vegetation as distinct from the physiology of the individual plant. This ought to be one of the most important branches of plant ecology, since it is clearly fundamental. Perhaps because this kind of work has been done mainly by plant physiologists, almost as a pastime, rather than by students primarily interested in vegetation, it has tended to lack coherence. I would suggest that such researches should be more directly related to plant communities whose general structure and behaviour are already known, or can be investigated at the same time. The field is both important and promising, and if we may judge from Mr Scott Russell's recent work in Jan Mayen, very good results can be obtained in a comparatively short time if the problems are properly tackled.

WORK IN NATURE RESERVES

One of the most troublesome and irritating hindrances to ecological observations intended to serve as a basis for the study of successional change, and therefore having to be spread over a series of years, is the liability to interference with or destruction of the vegetation of the area under observation by such events as clearing, felling, draining, gravel digging, change of ownership, or "development". I myself have twice had serial observations brought to an end by events of this nature in areas which I thought were safe from interference. It is therefore of great importance to have access to areas of varied vegetation which are absolutely safeguarded, and it was with great pleasure that the Council of this Society learned that the Forestry Commission proposed to reserve adequate areas which could be used for ecological work within some of the estates which they had acquired and that they had invited the co-operation of the Society. Accordingly representatives have been appointed to serve on a joint committee, and if the necessary workers become

available the results of their surveys and subsequent observations should not only substantially increase our knowledge of British vegetation but also be of considerable use to the Commission. This is indeed a great opportunity of which the Society should take the fullest advantage. I have long felt that similar opportunities were being missed in many of the properties of the National Trust. The fullest advantage has been and is being taken of the Trust Reserve at Wicken Fen and a great deal has been done at Blakeney Point, but there are many other Trust properties containing good natural or semi-natural vegetation suitable for ecological work but in which nothing is being done. I should like to see proper surveys of these instituted by the Society by arrangement with the Trust, and provision made for future periodic resurveys.

ANIMAL ECOLOGY

Of animal ecology I am not really competent to speak, even if I had the time. I hope we may soon have a President who will be able and willing to give us a review of the significant advances over a period of years in this rapidly developing subject. One point only I will mention. It has long been a dream of mine to see undertaken a thorough co-operative investigation of both the plants and animals of a definite habitat—a real penetrating study of how they live and what are their actual effects upon one another—in other words a comprehensive study of the biome of a well-defined, preferably of a relatively stable and mature, ecosystem, its conditions of existence, its structure and economy. The habitat would have to be very carefully chosen and so would the workers, for the job would need unlimited patience and ingenuity and would necessarily take a long time. I do not underrate its difficulty and complexity. But surely such an enterprise would be much more than worth while. I commend the idea to the Society.

HUMAN ECOLOGY

More and more frequently of late we have been hearing talk about “human ecology”, and it is evidence of the increasing attention that is being paid to the ecological point of view. We ought to ask ourselves how far the idea of applying ecological methods to human society may be valid. It is clear that in a general sense it must be valid. Human communities, equally with plant or animal communities, can only be intelligently studied in their proper environmental setting. A well-defined, localized human community is the kernel of an ecosystem just as is the plant community or the biome of any of the ecosystems I have considered in this address. Modern anthropologists have recognized this very fully and have published many studies of human communities in which the geographical, climatic and vegetational background of the community and the social and economic life which depends upon it have been given full significance. Some human communities are in relatively stable equilibrium, others are in process of rapid development; others again

are in disruption or decay, sometimes from internal, sometimes from external causes. In the phase through which humanity is now passing we see the trend towards internationalism, with world federation as its ultimate goal—the establishment of a world-wide ecosystem—arising inevitably from the increased interdependence of the people, the multiplication of the bonds between them, and the immensely increased rapidity of every sort of intercommunication. In violent conflict with this trend we see recrudescent nationalism, the desperate attempt to reintegrate by force the old national communities, many of which have become increasingly disintegrated. Unless indeed the human race shows itself ultimately incapable of effecting the new adjustments, the necessary next steps towards world-wide integration—and in that case it must relapse into disintegrated barbarism made all the more horrible by its scientific equipment—we cannot doubt the final issue of the conflict. The old human ecosystems are breaking down—many of them have already gone—and the only possible way to secure the positive human achievements of the past centuries is to make a new one which embraces the whole of humanity, retaining the more viable of the old partial systems, but subordinating them to the universal. I need not translate my words into political language.

So far the principles of ecology are unquestionably applicable to mankind. But when we come to consider methods of study we are at once confronted with the radical difference between human and non-human ecosystems introduced by the psychological factor, by the elements of self consciousness, will, reason, the moral sense, and the power of deliberate action directed towards a conscious goal. These, with the scientific knowledge and power man has acquired through their exercise, transcend and override the primitive adaptations he made to the original factors of his environment—geography, climate, soil, plants and animals. For these reasons the human ecologist, if we like to apply the word to the student of human society in the widest sense, must work with very different methods from those which we employ, though the basic principles are the same.

TECHNIQUE

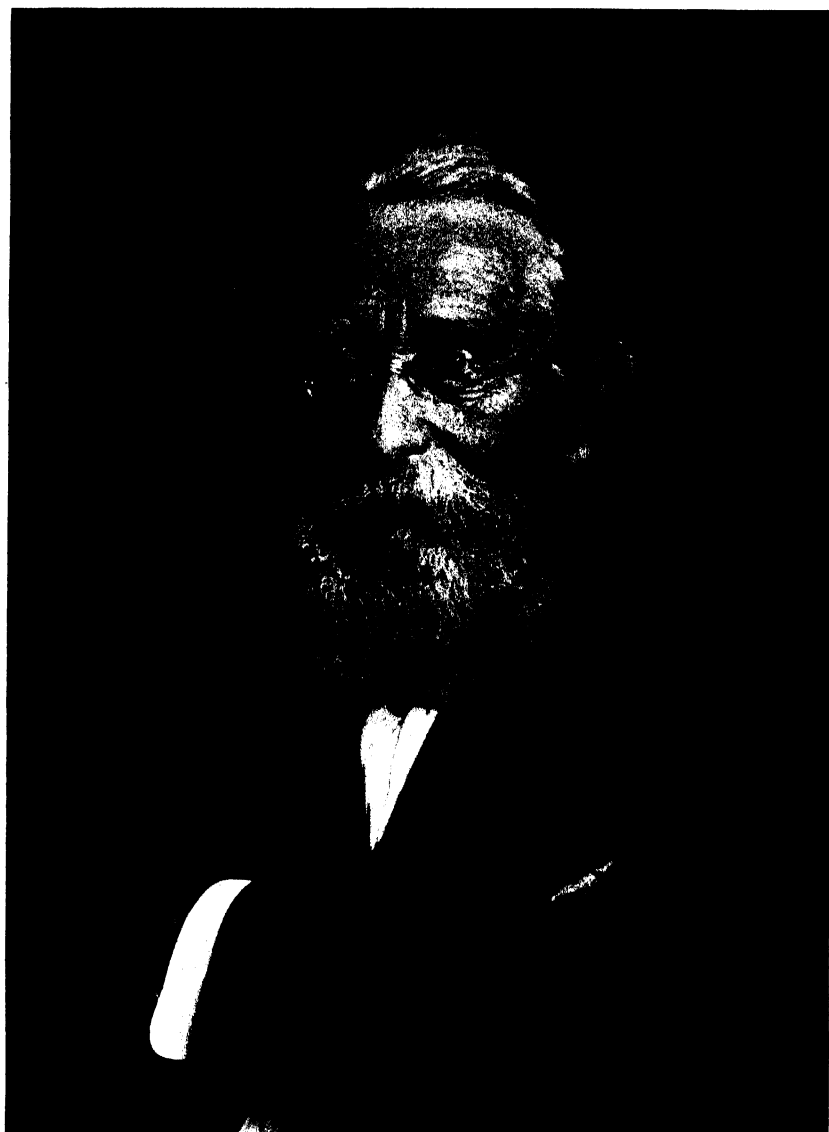
At the beginning of this address I referred to the difficulties of ecology. They are inherent in the nature of the subject, which, as I said, is not primarily a special branch of biology, like genetics, cytology or the physiology of nutrition, but rather a way of regarding living organisms, involving a constant effort to study them as they exist in nature, rather than to use them as subjects of specialized research. This essential difference is at once a serious disadvantage and a pre-eminent distinction of ecology. The disadvantage hinges mainly on the matter of technique. It is obvious that the progress of science depends very closely on technique, on the intelligent application of existing techniques and on the devising of new ones. The invention of a new technique

frequently leads to very rapid advance in knowledge and to the opening up of completely new fields. Every well-defined branch of biology develops its own techniques, so that beginners in the subject can use them from the outset; and if the worker is good enough he can apply them intelligently to new objects and perhaps go on to devise important modifications or completely new methods. In our subject there are very few important techniques which are distinctively ecological. I have already pointed out that the ecologist has to borrow and adapt the techniques belonging to different specialized branches of science. The study of the community or biocoenosis, the concept of which is the specific contribution of ecology, has not hitherto lent itself to the use of specific techniques, except of the very simplest nature.

The task of the beginner in ecological research is therefore much harder than that of the beginner in specialized branches of science. To do anything worth while he has to envisage his problems and devise means of attacking them from the very outset. He cannot apply a recognized routine technique while he gains knowledge and experience. I have constantly had to discourage students who said they wanted to "do ecology", to tell them that if they were keen enough they must choose some type of vegetation which seemed to present interesting problems and gradually learn by experience how these could best be attacked. That sort of counsel chokes off the weaker brethren altogether, and this of course has its advantages because it ensures that only those who have real enthusiasm for the subject and a consciousness of ability to think for themselves will persist in undertaking ecological work. A minor but quite real academic drawback is the frequent necessity of spending long working periods in the field, which does not fit in well with existing academic regulations.

PROSPECTS

More serious is the difficulty of placing the young ecologist in a bread-winning job. Compared with the mycologist and even with the plant physiologist or geneticist he is still at a grave disadvantage. I cannot but believe, however, that this particular handicap will eventually disappear, since I have no doubt whatever that ecological training, of course on a sound basis of fundamental biology, is the best of all preparations for a number of practical activities—for scientific forestry, for the pastoral industry and for the proper use and administration of undeveloped lands in "new" countries—for all those industries, in fact, which are based on natural and what we call "semi-natural" vegetation. Recognition of this has recently begun to penetrate to those in authority, and a few appointments have been made. Progress in such recognition is slow, but I have confidence that it will be continuous, because I am quite sure that it is soundly based. Meanwhile, in the long run, we shall get what we deserve—no more and no less—and it is up to us to see that we deserve a great deal.



C. Schröter

CARL SCHRÖTER, AETAT 70

OBITUARY

CARL SCHRÖTER, 1855-1939

ON the 7th of February, in his 84th year, Carl Schröter died at his home in Zürich after three or four days illness—an attack of influenza followed by pneumonia. So ended a long and extraordinarily happy life, filled to the utmost with useful and beneficent activity.

Schröter's connexion with our Society was very close. In July 1908 he led an excursion through Switzerland for the study of its vegetation, organized in connexion with the International Geographical Congress of that year; and it was the brilliant success of that excursion, due to Schröter's wonderful leadership, which inspired the organization of the first International Phytogeographical Excursion (I.P.E.) through the British Isles in 1911. The Swiss botanists have since taken these Excursions under their especial care. The first I.P.E. was organized by the British Vegetation Committee—a modest association of keen students of vegetation started in 1904—and it was the widening and deepening interest and enthusiasm for the subject, aroused largely by that successful achievement, which led to the transformation of the Committee, in 1913, into the British Ecological Society. Schröter, with his pupil and disciple Rübel, came to England as representing Switzerland on the Excursion of 1911, and took the closest interest in the work of the British Committee and the subsequent foundation of the new Society. In 1925, on the occasion of Schröter's 70th birthday, the Society unanimously elected him an Honorary Life Member—a distinction reserved for very few—as an expression of their gratitude and of their admiration for his work and personality. In 1930 he came again to England to attend the International Botanical Congress at Cambridge, and on that occasion his English friends were delighted by the conferment upon him of the honorary degree of Sc.D.

Carl Schröter came of a family belonging to Bielitz in Silesia, and was born in 1855 at Esslingen near Stuttgart, where his father, Moritz, was an engineer. In 1865 Moritz was appointed Professor of Machine Construction at Zürich, to which he migrated with his family. After the death of Moritz in 1867 the town conferred the citizenship of Zürich on his widow and children, and from that time Carl became completely Swiss, not only legally but in spirit.

In 1876 Carl qualified as a teacher in natural science at the Eidgenössische Technische Hochschule, and two years later began to lecture on "special" botany as assistant, under the ordinary Professors of Botany, Carl Cramer and Oswald Heer, soon afterwards taking over the whole of the work in that branch. From the first Schröter made field excursions a leading part of his teaching, and worked extremely hard to acquire not only a knowledge of the

names of species, but of everything interesting he could find out about them. The extraordinarily wide and thorough knowledge of plants he thus acquired redounded to the benefit of his students through many years of teaching activity. In 1880 he took his doctorate with a thesis on some of Heer's fossil plants from the Arctic, and after Heer's death in 1883, on his 28th birthday, was appointed ordinary Professor for "special" (i.e. systematic) botany, a post he held till his retirement in 1925.

Schröter's untiring energy and enthusiasm made him both a wonderful teacher and an unremitting investigator. His actual technique of lecturing was extremely successful and his students made rapid progress. He dealt mainly with the flowering plants, and since he had to teach foresters and agricultural students, largely with trees and grasses. His exposition of systematics was a joy to listen to, escaping entirely from the wearisome atmosphere so frequent in the teaching of this subject.

Besides general systematic botany Schröter taught, for a time, economic and pharmaceutical botany, and as early as 1882 he took up plant geography, which was later to become his main interest. It was Christ's *Pflanzenleben der Schweiz* and Kerner's *Pflanzenleben* and *Pflanzenleben der Donauländer* which helped to turn Schröter's interest in this direction, and beside these we were able to put, in 1908, his own great work *Das Pflanzenleben der Alpen*. As the years went on he lectured on many branches and aspects of phytogeography, taking an increasing interest in the ecological side, and as the result of his world tour in 1898-9 he prepared a general course based on his observations and collections, including not only the vegetation, but the native populations and their culture, and this attracted such large audiences that it often had to be given twice in one year. He began to lecture on the flora and plant geography of the Alps themselves quite early in his career: this was always his favourite subject on which he soon became the leading authority.

His field excursions were especially fine—carefully organized so that the students of special branches, as well as the general students of botany, derived the greatest profit from them, and the whole were informed by Schröter's immense knowledge and field experience and also enlivened by his never-failing good humour and high spirits. His exuberant boyishness in the field, his yodelling, songs and jokes in the intervals of serious work, were a constant source of delight to everyone fortunate enough to be his companion, and his students worshipped him.

Schröter's researches touched many fields, though "geobotany" was eventually his chief absorbing interest. At the outset of his career he worked on geotropism and the history of germination in the broad bean, and later, besides contributing many papers on morphological-systematic topics he wrote on limnology and plankton, on palaeobotany, on scientific travel and on the protection of nature. Of his larger published works, independent or joint, the *Beiträge zur Kenntnis der Matten und Weiden der Schweiz* (with

F. G. Stebler), 1887–93; *Die Vegetation des Bodensees* (with O. Kirchner), 1896, 1902; *Das Pflanzenleben der Alpen*, 1904–8 (second edition, 1923–5); *Die Moore der Schweiz* (with J. Früh), 1904, are some of the more important. Besides these he published in 1889 the very useful and attractive *Taschenflora des Alpenwanderers*, with coloured plates and German, French and English text, which has gone through many editions; and in 1936 (one of his latest works) *Flora des Südens*, with German, French, Italian and English text, dealing with “Insubria”, the district lying immediately to the south of the Alps; as well as important articles on Phytogeographical Maps, on Genetic Plant Geography, on the Flora of the Swiss National Park; and very numerous smaller contributions. Schröter was also joint editor of the series *Lebensgeschichte der Blütenpflanzen Mitteleuropas*, to which he contributed several articles, especially on coniferous trees.

One of Schröter’s great activities was in connexion with the Schweizerische Naturforschende Gesellschaft, an important body corresponding with the scientific “academies” of other countries, and responsible for the foundation of many “commissions” which organize systematic research and publication of the results in various branches of science, really doing the work of “National Institutes” in other countries. To several of these commissions Schröter gave yeoman service, as member, secretary or president, and the total amount of work involved in these activities alone must have been colossal. Into the work of the Commission for the Protection of Nature and its leading task—the establishment of the great Swiss National Park in the Lower Engadine—he threw himself with special energy and devotion. He gave innumerable lectures and wrote articles in all possible journals on the beauty and interest of the National Park and thus acquired thousands of members for the Swiss Society for the Protection of Nature. He also took over the direction of the scientific investigation of the National Park as President of the Commission formed for this purpose in 1915, and the accumulating results have brought a rich return with the passing years.

But even above all this rich and fruitful talent and scientific achievement we must rank Schröter’s character as a human being. His was one of those rare personalities which radiate light and warmth on all their surroundings. On students, colleagues, friends and on every one with whom he came in contact he lavished a dynamic kindness and helpfulness, and one never met him without going on one’s way cheered and encouraged. A little incident in England in 1911 will illustrate his overflowing kindness. Noticing that two middle-aged ladies were likely to be neglected and lonely on the occasion of an evening reception, he devoted himself to their entertainment for the entire evening, though he was surrounded by friends and colleagues who would have been delighted to spend their time with him. At his Institute in Zürich there was no formal “consultation hour.” From morning to night, so long as he was there, any one came at any time and took what he could give—friendly

counsel and advice, encouragement to scientific work. Everyone knew that he would value the smallest observation or contribution to knowledge, and would know how best it could be used. As Rübel wrote of him in 1925: "Für ihn liegt der Zweck des Lebens im Geben. Alles, was er weiss und kann, freut ihn nur, wenn er anderes daran teilnehmen lassen kann, so stellt er sich in den Dienst der andern, in den der Allgemeinheit."

Schröter was very happy and fortunate in his marriage. His wife, an old fellow-student, was able to understand and support her husband as investigator, teacher and human being. She saw to it that their house in the Merkurstrasse was always open to his friends and colleagues, to the botanists of all countries. And at the same time he found in his home rest and refreshment which enabled him to keep his freshness and youthful vigour to the end. His departure from amongst us leaves a gap which cannot be filled, but also a very dear memory which will continue to stimulate and inspire every one who was fortunate enough to know him.

The writer is deeply indebted to Rübel's article in the *Carl Schröter Festschrift* (1925), from which a great deal of his information is derived.

A. G. T.

REVIEWS

THE JOURNAL OF ANIMAL ECOLOGY

VOL. 8, No. 1, MAY 1939

THIS number contains twelve papers dealing with terrestrial, freshwater and marine ecology, and with ecological theory; also ten reviews, 188 Notices of Publications on the Animal Ecology of the British Isles, and the Society's business and address list of members: 225 pages altogether. There is an important survey of the habitat distribution of British woodland birds, organised by D. Lack and L. S. V. Venables for the British Trust for Ornithology, including 152 woods in summer and 120 in winter. Most of the habitat preferences are the same as those on the north European mainland, and deciduous and coniferous woods, though showing certain well-marked differences, both have a rich bird fauna. A smaller study of habitat selection among birds in Lapland birch woodland, by H. N. Southern and L. S. V. Venables, brings out the importance of seasonal factors, such as snow melting, in determining the nesting habitats chosen. R. S. McDonogh contributes a thorough survey of the distribution and habitats of a small wingless moth, *Luffia ferchaultella*, which lives on lichens on tree trunks in southern Great Britain. W. L. Taylor records the distribution of wild deer in the woodlands of England and Wales, and shows that the numbers have been increasing with the progress of afforestation, and that three foreign species of deer are establishing themselves along with the three British ones. There are two important studies of succession. The first is by H. B. Moore, who records the species of marine plants and animals colonizing a bare area of rocky shore near Plymouth. He concludes that the order of colonization is less important than the conditions at the time of settling. The second study is by K. D. Baweja, who conducted elaborate controlled experiments upon sterilized soil plots and made population counts of the invertebrate species colonizing them. The populations reached higher levels in the sterilized plots than in the controls. Another soil study, by A. Dixon, gives lists of Protozoa from soils collected by the Wagers' Expedition in East Greenland. The soils with richest vegetation have the highest number of species. Most of these soils are frozen for nine months of the year.

C. Matheson discusses the status of the colonies of the black rat (*Rattus rattus* and varieties) in British sea-ports, and gives convincing evidence that these colonies are permanently maintained on shore and do not depend on continued arrivals from ships. P. H. Leslie and D. H. S. Davis analyse the population density of a rat population in Sierra Leone. A theory of random collisions between rats and traps is evolved, which is of general importance. Freshwater studies include one on the flooding factor in European caves, by R. S. Hawes, and another on the food of the pike in Windermere, by K. R. Allen. There is an entertaining description by E. P. Smith of the introduction and spread and subsequent recession of edible frogs (*Rana esculenta*) in East Kent, which illustrates some of the unpredictable effects of such introductions. Reviews deal with the Journal of Ecology, a new Russian text-book of ecology by Kashkarov, animal population problems, breeding seasons in man and animals, a Californian wren-tit population, the flight of birds, small islands and British freshwater animals. The Notices, done by thirteen voluntary workers, again cover most of the important publications on the subject of animal ecology in the British Isles.

CHARLES ELTON.

BRITISH EMPIRE VEGETATION

Bayer, A. W. *An Account of the Plant Ecology of the Coast-belt and Midlands of Zululand.* 2 text-figures, 5 plates. *Ann. Natal Mus.* **8**, 371. 1938.

This paper contains a fairly full account of one of the less well-known parts of South Africa and also gives some useful data for some climatic features. Thus extremely low values for the relative humidity of the air are here recorded, values of as low as 7–10% of saturation having been obtained at midday in conjunction with high temperatures. Such figures apply mainly to the interior, more humid conditions being maintained in the coastal belt, for, speaking generally, south-east winds tend to be prevalent and there is increasing desiccation as the interior is reached.

Much importance is attached to the very marked effects of cold-air drainage in producing local climates. This factor may control not only the incidence of frosts but also the distribution of mists in the valleys, and a good correlation is claimed between these factors and the distribution of more humid vegetation types. The other factor affecting the local climates is the aspect, for south-facing slopes appear to be affected not only by the greater humidity of the south-east winds but also are less insulated and apparently more subject to mist. As a consequence they commonly bear woodland communities rather than grassland or scrub.

The vegetation of the coastal belt and the midland area are treated separately, and lists of the more important species in the different communities are given. Attention is drawn to the very characteristic dwarfed habit of the woody plants in some types of veld (e.g. Mobola veld). The view is taken that this is not due to the effects of wind, for normal plants are absent even in sheltered places. A number of factors may operate and possibly different ones may affect different species.

The climax grassland community in the midland area is the *Themeda triandra*-*Hyparrhenia hirta* association. This is preceded by tufted xerophytic grasses with various geophytes and succulents, and then by a stage in which *Eragrostis plana* and *Sporobolus indicus* are dominant. The general effect of burning and overgrazing is to throw back the succession from the *Themeda*-*Hyparrhenia* stage to the less nutritious *Eragrostis*-*Sporobolus* community. Similarly, the latter community is common in the farming areas, but where, owing to the presence of tsetse fly, stock is absent, *Themeda* becomes the characteristic grass.

Various other effects due to grazing are mentioned and a considerable number of possible biotic influences are described. The evidence is held to suggest that the effects of wild animals may have considerably decreased. Fires also are given a somewhat more limited role than has often been the case, for they are supposed to prevent the extension of forest rather than to destroy it.

W. H. P.

Blake, S. T. *The Plant Communities of Western Queensland and their Relationships, with Special Reference to the Grazing Industry.* 19 plates, 2 maps and 2 text-figures. *Proc. Roy. Soc. Queensland*, **49**, 156. 1938.

This paper gives data for the climate and soils of Western Queensland and a detailed account of the main vegetation types in the area. Using the terminology of Clements the author recognizes the following groupings:

I. Open forest formation, which includes a *Eucalyptus* forest and a mixed *Eucalyptus*-*Acacia* ericoid shrub association on the Great Dividing Range.

II. Closed forest formation, including two associations, Ooline forest (*Cadellia pentastylis*) and mature Brigalow scrub (*Acacia harpophylla*). Farther east this includes true rain forest.

III. *Acacia* scrub formation, including Gidgea scrub (*Acacia Cambagei*), Mulga (*A. aneura*) and Lancewood (*A. Shirleyi* and allied species).

IV. The *Triodia* (Spinifex) formation, with four well-defined associations:

- (i) *Eucalyptus pallida*-*E. leucophylla*-*Triodia* association.
- (ii) Desert sandstone association—*Triodia* communities with *Eucalyptus normantonensis* and *Acacias* of III.
- (iii) The Spinifex sand plain.
- (iv) An association with *Triodia irritans* or allied species.

V. The grassland formation, with four associations:

- (i) The blue grass association.
- (ii) The ashy downs-Mitchell grass association.
- (iii) The gravelly downs-Mitchell grass association.
- (iv) A steppe association with herbs (*Atriplex* and *Bassia*).

VI. The channel country formation, including fringing forest *Eucalyptus* spp., herbaceous communities of the alluvia, salt bush (*Atriplex nummularia*), some cotton-bush and samphire communities and clay pans. All are dependent on periodic flooding.

VII. The swamp formation.

VIII. The shrub steppe formation, which includes the *Kochia planifolia* association, the *Atriplex vesicaria* association and the cotton-bush communities (in part).

IX. Desert.

A point which is stressed is that almost throughout Queensland, the vegetation is of an unstable nature so that it is frequently difficult to state what are seral and what are true climax communities. It has been shown in West Queensland that these changes are oscillating and not progressive, but what the factors are which produce the oscillations is uncertain. Rainfall and, since settlement, stocking appear to be two of the factors indirectly concerned and it is regarded as possible that cyclic variations in the salt content of the soil may also be important. Whatever these factors may be they produce striking variations in the carrying capacity of the country and hence may be of great economic importance.

In addition to the communities recognized above, a series of induced communities is described, mainly those around bore-holes and along the great stock routes.

A good coloured vegetation map is given and also a tentative soil map, apparently based very largely upon the author's own observations.

W. H. P.

VEGETATION OF NEW ZEALAND

- (1) *An Outline of the Vegetation and Flora of the Tararua Mountains*. By V. D. Zotov, A. D. Beddie, G. O. K. Saunbury and E. A. Hodgson. *Trans. Roy. Soc. N.Z.* 68, 259. 1938.
- (2) *Some Correlations between Vegetation and Climate in New Zealand*. By V. D. Zotov. *N.Z. J. Sci. Tech.* 19, 474. 1938.
- (3) *Survey of the Tussock-grasslands of the South Island, New Zealand*. By V. D. Zotov. *N.Z. J. Sci. Tech.* 20, 212a, 1939. (Bull. 73, Dep. Sci. Industr. Res.)

These three papers deal with various aspects of New Zealand vegetation and with similar groups of problems. The first paper is mainly descriptive, giving lists of Spermatophytes, Pteridophytes, and Bryophytes for the range of mountains known as the Tararuas. There is also, however, a review of the main climatic features and of the ecological relations of the vegetation. The latter shows very clear altitudinal relations, and it is considered that temperature plays a main part in controlling these. Much importance is also attached to fog and cloud level, which is found to reduce the light to a very low intensity and in this way is considered to control the timber line, largely through the failure of the dominant tree,

Nothofagus Menziesii. This regenerates at higher levels but is unable to maintain itself. Rainfall also appears to have some importance, particularly in regard to the distribution of the various species of *Nothofagus*. Striking wind effects are also recorded.

In addition to the various plant communities on areas undergoing erosion or sedimentation, the following main (apparently climax) types are described:

(1) Warm temperate forest (0–600 m.) in which the dominant trees are *Metrosideros robusta* or *Dacrydium cupressinum*.

(2) Cold temperate forest (600–1200 m.) in which *Nothofagus Menziesii* and *N. fusca* are usually the dominants, the latter particularly below 900 m. and the former above.

(3) Cold temperate scrub which is dominated by various shrubs and most often by *Olearia colensoi*.

(4) Warm sub-polar belt: tussock. This is a grassland dominated by forms of *Danthonia antarctica*. It changes on the steeper slopes to *herb field*, with a variety of species, and on the few flat-topped hills and shoulders to a form of *fell field* of cushion, rosette and adpressed plants.

It will be seen that the main factor employed in delimiting the climax communities is altitude, and the point of view adopted is developed further in the second of the two papers cited above, in which it is proposed to define the vegetation belts by the distribution of species rather than of communities. Evidence is given that the altitudinal belts are determined by summer temperature rather than by factors such as the duration of winter snow. The distribution of species of *Nothofagus* and the causes of the timber line are considered from this point of view. As a result of this discussion various modifications of Cockayne's limits and his botanical districts are suggested.

The third paper, a survey of grasslands, is in many respects the most important of the series. The author regards the tussock-grassland on the east of the South Island as a form of steppe and shows that both vegetation and climate conform to the essential requirements, with peculiarities such as high wind velocity and low summer temperatures. Much of the existing tussock is induced, not natural, and a reconstruction of the original vegetation is given, with a map showing the probable limits of true steppe and the known limits at the time of the earliest settlers. Much of the present tussock-grassland is on the site of forest (*Podocarpus* or *Nothofagus*).

Although forms of *Festuca novae-zealandiae* give a very characteristic appearance to large areas, in protected places, varieties of *Agropyron scabrum* tend to replace the fescue almost entirely. Even the hardier species associated with fescue are not able to hold their own under the treatment which is meted out to them, and very large areas of former grassland are now semi-desert and problems of the control of this degeneration and of the associated problems of soil erosion have become almost universal. The prime factor in this series of changes is not overgrazing so much as the frequent burning, carried out ostensibly to reduce the incidence of valueless weeds and to increase the palatability of the fescue. This gradually and inevitably destroys all the vegetation of value and allows the destruction of the humus. The bearing of these findings on the question of grassland regeneration and their responsibility for much of the damage attributed to rabbit attack, is discussed at some length. W. H. P.

GENERAL TREATISES

Miller, E. C. *Plant Physiology, with reference to the Green Plant*. Second edition.

Pp. 1201 + xxxi, with 39 figures in the text. New York and London: McGraw Hill. Price 45s.

The border between ecology and physiology is often narrow and sometimes non-existent, although otherwise the ideals and content of these aspects of botany may diverge very widely. Thus a treatise on plant physiology may or may not appeal to ecologists, depending

primarily upon whether its outlook includes any considerable treatment of the plant-habitat relation or not. Undoubtedly two sorts of books on plant physiology may be useful to the ecologist—one, the type which deals primarily with these aspects of ecological physiology or vice versa—and the other, which is primarily a work of reference, from which may be gleaned information on all the physiological problems which an ecologist may encounter. Of these two fields, the former has been developed by Lundegårdh in his well-known book. In the second field, Prof. Miller's book must certainly be given pride of place, for it contains a maximum of reference to original work and a minimum of personal opinion.

The present second edition of this work is, in fact, remarkable in this connection. It has been greatly extended and much improved and at a rough estimate contains 50% more matter than the first edition, probably more. The list of references is extremely full and they are well marshalled in the text. Possibly the American literature is more fully represented than the European, though this is understandable. There are good subject and author indexes.

As far as the subject matter is concerned, it may be well to emphasize the fact that in spite of the size of the volume no treatment of irritability and plant movements is attempted. Three main groups of topics are considered—water and salt relations, metabolism, and growth. General and field methods of investigation receive adequate attention, and of particular value to the ecologist are the full summaries of such particular features as atmometry, soil and water properties in relation to plants, root systems, and the like.

W. H. P.

Ashby, H., Ashby, E., Richter, H. and Bärner, J. *German-English Botanical Terminology*. Pp. 195 + xi. London: Thos. Murby and Co. Price 10s.

This book also is included here, for though it is not primarily ecological it is an unusual one and a work of great utility. It consists of parallel texts in English and German, employing the equivalent words in their normal meanings and contexts. These texts give a brief but wide survey of botanical subjects under the headings, morphology, classification and phylogeny, cytology and genetics, physiology, ecology and plant pathology. The ecological section, for example, deals, in eighteen pages, with the terminology of such subjects as environmental factors, including soil types and properties, the analysis of vegetation, life forms, quantitative description, classification and development of vegetation, the definition of characteristic English and German vegetation types.

These descriptive chapters make up the bulk of the book but there are also three appendices, the first giving English and German and Latin names of common wild and cultivated plants in Europe; the second, lists of the equivalent names of plant diseases, and the third the abbreviations commonly used in English and German botanical literature. The book should certainly be of great value to students and of considerable utility to more experienced workers.

THE VEGETATION OF MOROCCO AND WESTERN ALGERIA

Rübel, E. and Lüdi, W. (edited by). *Ergebnisse der Internationalen Pflanzengeographischen Exkursion durch Marokko und Westalgerien*, 1936. Pp. 258, with 18 photographic plates and a coloured vegetation map. *Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich*, 14. Heft. [Verlag Hans Huber, Bern.] 1939. Price 12·50 Swiss francs.

Among the many valuable services rendered to geobotany by the Rübel Institute, the publication of the results of successive International Phytogeographical Excursions is not the least; and this account of the eighth I.P.E. is perhaps the most interesting and in-

formative of the series. The satisfactoriness of the composite work is largely due to the admirably lucid and comprehensive description of Moroccan vegetation (pp. 40–157) by Prof. Louis Emberger (formerly of Rabat, now Flahault's successor at Montpellier) and his map of the vegetation on the scale of 1 : 1,500,000. These form a solid background to the essays by other members of the international party on various aspects of the vegetation.

The map attempts to represent the "primitive" state ("climax") of the vegetation, the existing plant covering being the "miserable remains" of the original condition. The native agriculture does not completely destroy all traces of the primitive plant communities, so that it is still possible to reconstruct these, at least in their main outlines. The following brief summary is based on Prof. Emberger's "Aperçu général".

The climate of the whole of Morocco is essentially "mediterranean", i.e. the hot season coincides with the dry season, the rains being confined or nearly confined to the colder season. This is true even on the summits of the high mountains and even in the extreme south where the Mediterranean climate passes into the desert climate of the northern Sahara with total rainfall reduced to an insignificant amount. However, the climate of the country is also oceanic, i.e. the ranges of temperature are *relatively* slight, though the north and west, in proximity to the Atlantic and the Mediterranean, are of course much *more* oceanic than the high plateaux and summits of the east.

With the help of a formula in which the factors of total precipitation (P), mean maximum of the hottest month (M) and mean minimum of the coldest month (m) are included, Emberger distinguishes the following varieties of Mediterranean climate: Saharan, arid, semi-arid, subhumid, humid, and high mountain. Each of these may be warm and oceanic (with m high) or cold and continental (with m low). To each of these climates belongs a group of plant communities with equivalent ecological requirements, but the dominants vary in their plasticity, so that some (*Quercus ilex*, for example) extend through more than one type of climate, while others (e.g. *Juniperus thurifera*) are strictly confined to one.

Physiographically Morocco is dominated by mountain ranges—the coastal chain of the Rif in the extreme north, abutting on the Mediterranean, and connected by hill country to the south with the great chain of the Atlas. The general trend of the Atlas range is E.N.E. and W.S.W.: it consists of the great central ridge of the High Atlas exceeding 3000 m. in height, including the loftiest summits of more than 4000 m. and extending westwards to the Atlantic; the "Anti-Atlas", which forms a diverging south-western wing of the High Atlas; and the "Middle Atlas", a similar diverging north-eastern wing connecting northwards through hilly country with the Rif. Eastwards the Middle Atlas is continuous with the Algerian "Tell" or "Little Atlas", while the High Atlas passes, with greatly decreasing altitude, into the Algerian "Sahara Atlas". Between the Rif and the High Atlas towards the Atlantic is a great plain (in the south of which lies the old southern capital, Marrakesh or "Morocco City") broken here and there by low hills and occupying more than a third of the whole country. This has an altitude of more than 1000 m. in its eastern portions and gradually falls towards the Atlantic coast. Between the High Atlas and the Anti-Atlas is the well-defined plain of the Sous, with Agadir in its north-western corner, lying against the seaward buttresses of the High Atlas. South and south-east of the Anti-Atlas and High Atlas lies the desert.

The Saharan or desert vegetation is only represented in the extreme south of Morocco, and was visited by the Excursion in southern Algeria.

Arid climate. The arid Mediterranean climate with mild winters is characterized by forests of the remarkable endemic sapotaceous tree *Argania spinosa*, which occupied (and still occupies part of) the plain of the Sous, and the south-western coastal strip behind Safi and Mogador. Most of the existing Arganietum is not however in a natural state, but is really a cultivated community, almost comparable with the Oleëtum of the Mediterranean region at large. Most of the Sous is now quite destitute of trees, villages such as Tiznit (the most

southern point visited by the Excursion) having all the character of genuine oasis settlements in true desert, with date palms and irrigated barley cultivation.

Other characteristic trees of the mild arid climate are the endemic *Acacia gummifera* with *Pistacia atlantica* and *Zizyphus lotus*, which together form an association that was once of very wide extent in western Morocco but is now mostly destroyed. The *Argania* forest still remains over wide stretches because it is useful, especially the oil of the fleshy fruit which is employed for a great variety of purposes. The others only exist here and there. Farther eastward, where the winter is cold, the trees are absent (owing not to low temperature but to aridity) except along watercourses, and the vegetation is "steppe" dominated by *Stipa tenacissima* (the economically important "halfa") and *Artemisia herba-alba*, which occupy vast areas in the high valley of the Moulouya between the Middle and High Atlas, and eastwards into Algeria on the high plateaux of the "sud-Oranais", between the Tell and Sahara Atlas. Prof. Regel objects to this vegetation being called "steppe", pointing out that it has little in common with the characteristic chernozem or "black earth" steppes of southern Russia, to which he thinks the name should be restricted. The Halfa steppe has extended its area owing to the destruction of semi-arid forest, e.g. of *Juniperus phoenicea* or *Callitris* (*Tetraclinis*).

Semi-arid climate. The semi-arid region is the largest of the climatic regions of Morocco. It occupies most of the Atlantic plains except the Sous and the enclave of Haouz-Tadla, and it also encircles the Rif and the Middle and High Atlas, isolating more humid areas, as well as forming islands in the arid region. The rainfall is higher or the summer temperatures lower than in the arid region, leading to diminished evaporation. Again we have differences determined by mild, temperate, or cold winters (mean minima above, around, or below 0° C.).

The vegetation of the semi-arid regions with mild winters has very various woody dominants (*Callitris*, *Pinus halepensis*, *Argania*, *Quercus suber*, *Q. ilex*, *Q. coccifera*, etc.); with temperate winters *Juniperetum phoeniceae*, with cold winters *Juniperetum thuriferae*. The dwarf palm *Chamaerops humilis* is characteristic of the temperate and mild semi-arid climate. *Callitris* (*Tetraclinis*) is strictly limited to the mild semi-arid climate, *Juniperus thurifera* to the winter-cold type. The other dominants are climatically more plastic.

The woods of *Callitris* are confined to Morocco and western Algeria, with the exception of small fragments in Malta, Cyrenaica and southern Spain. They form a characteristic rather open forest, which fringes the northern side of the Anti-Atlas and the western and northern slopes of the High Atlas. There are also considerable areas in the north, including the eastern end of the Rif, but much has been destroyed. *Callitris* is on the whole indifferent to soil, but as the climate becomes damper the woods are confined to limestones, being ousted by the cork oak, the olive and the lentisk on siliceous and argillaceous soils.

Pinus halepensis is relatively rare in Morocco, and most of it is in the east, on slopes towards the Mediterranean, with some on the northern slopes of the Middle Atlas and islands on the High Atlas. It also occurs on the higher summits of the Algerian Sahara Atlas. It is largely a relict, but certain islands of it have become centres of new dispersal owing to the destruction of surrounding vegetation. In this way the Aleppo pine is now invading some of the degraded cedar forests. It is a little less xerophilous than *Callitris*, so that it tends to yield to the latter in eastern Morocco as the forests are degraded, while in the west forest destruction favours its spread.

Various dominants of other climates extend into the semi-arid region with mild winters under certain conditions, *Argania* from the arid type, the evergreen oaks from the sub-humid and humid.

The two junipers (*Juniperus phoenicea* and *J. thurifera*) are characteristic respectively of the semi-arid climate with moderate winter cold (mean minimum around 0° C.) and extreme winter cold (mean minimum well below 0° C.). *J. phoenicea* (the red juniper) is

edaphically indifferent, and everywhere replaces *Callitris* as the winter temperatures fall. In the mild west it is abundant on the sand-dunes, where it follows *Ammophila* in the succession, and is not subject to the competition of *Callitris* or *Quercus ilex*. As we pass eastward on the High Atlas the red juniper inserts itself more and more abundantly between the *Callitris* woods below and the *Quercus ilex* woods above, and once also formed a broad belt on the southern slopes; but this is almost entirely destroyed. *Juniperus phoenicea* is also one of the chief dominants farther east on the upper slopes of the Sahara Atlas in Algeria. *J. thurifera* replaces *J. phoenicea* as the climate becomes more continental, and especially colder in winter. The tree is absent from the Rif and from the oceanic western end of the High Atlas. In the Middle Atlas it is widespread, but by far the greatest part is in the High Atlas, attaining at least 3000 m. altitude, and often forming the upper limit of forest.

A great belt of country in the north-west of Morocco is, or rather was, largely occupied by low forest or scrub of *Olea*, *Pistacia lentiscus* or *atlantica* and *Chamaerops humilis*. The *Olea-Pistacia* scrub is strictly localized on heavy compact clay soils, and is for the most part destroyed because it occupied ground which was the most fertile and the easiest to cultivate. When the soil is rocky or sandy the scrub gives way to forest of *Callitris*, *Quercus suber* or *Q. ilex*. The *Olea-Pistacia* scrub, though with different associates, also occurs in the subhumid region. The ultimate stage of degradation of this scrub is dominated by the dwarf palm *Chamaerops humilis*, which often almost covers the ground with its vegetatively propagated shoots. This community is very rich in herbaceous species with brilliantly coloured flowers and includes a large number of monocotyledonous geophytes. The dwarf palm avoids regions which are too moist or too dry, and only grows where the mean minimum of the coldest month is above 0° C. It is thus absent from the higher altitudes and from the dry slopes towards the south-eastern desert. The distribution of *Chamaerops* in Morocco is strikingly complementary to that of Halfa (see sketch-maps on pp. 150, 154) which dominates the eastern high, dry and winter-cold steppes.

Arganietum extends from the arid into the mild semi-arid region, and the evergreen oak forests, which are most at home in the humid and subhumid regions, also extend into the semi-arid. The great forest of Mamora near Rabat is the best example of a cork-oak forest on sandy soil in the semi-arid region. While *Quercus suber* is, in Morocco, a tree of the plains and low altitudes, *Q. ilex* belongs to the mountains. It can tolerate a wide range of climate, but semi-arid holm oak forest is rare. South of Rabat it exists however on siliceous rock between the belts of cork oak and *Callitris*.

Subhumid climate. The subhumid Moroccan climate may be considered as the mean Mediterranean climate. It is the climate of Mediterranean France, of Catalonia, and of much of Italy, and classical Greece, i.e. of the regions that we first think of when Mediterranean climate and vegetation are mentioned. In Morocco, except in certain parts of the north where the rainfall is relatively high, the subhumid climate is restricted to the mountains—the Rif, the Middle Atlas, medium altitudes on the northern slopes of the High Atlas, and the western end of the southern slope, with an island on the western end of the Anti-Atlas, where the highest ridges receive sufficient rain and are not too hot. The total area is considerable but much less than that of the arid and semi-arid climates.

The plant communities of the subhumid climate are much fewer than those of the semi-arid. *Quercus ilex* is by far the most important dominant, with *Q. suber* occupying a second place. *Pinus pinaster*, *Quercus faginea* and even *Cedrus atlantica* come into it, but are much better developed in the humid climate. A form of the *Olea-Pistacia lentiscus-Chamaerops* scrub also occurs.

Almost all the *Quercus ilex* in Morocco (still amounting to about 700,000 hectares, while much more has disappeared) occurs in the subhumid climate of the lower slopes of the Rif and the north-western slopes of the Middle and High Atlas. In the damp climate of the Atlantic slopes of the Rif the holm oak is strictly confined to calcareous soil, being excluded

on other soils by the competition of the other oaks. The subhumid *Quercetum ilicis*, when intact, forms a low, very dense, almost closed forest with little undergrowth, but it is usually semi-open, and then has many more species. Various distinct communities can be separated, characterized by the possession of different endemics and other associated species, and corresponding with warmer and cooler climates, calcareous and non-calcareous rocks.

The other evergreen oaks are much less important. *Quercus coccifera* is rare in Morocco, being confined to the Mediterranean slopes of the Rif. It is generally a richly branched shrub, but in the mountains of Ceuta it is arborescent, so that one can walk under its shade, and here it forms an autonomous community with *Taxus baccata*. *Quercus suber* appears in the scrub of *Olea-Pistacia-Chamaerops* where the soil is less clayey, bringing with it such characteristic silicolous plants as *Arbutus* and *Erica arborea*, but scarcely forming an oakwood. This set of communities differs from those with the same dominants in the subarid climatic region by the possession of a rich collection of familiar species of the European maquis and including also plants of cool temperate European climates like *Hedera* and *Crataegus monogyna*, as well as several endemics.

Pinus pinaster belongs especially to the humid Mediterranean climate, but it forms woods of some importance in the subhumid region. In Morocco it is always a mountain tree, occurring from 1000 m. to 1900 m. in the Rif, and from 1500 to 2200 m. in the Middle and High Atlas. It can grow on both calcareous and siliceous soils, and this behaviour is interesting, to compare with its occurrence in Provence, where it appears to be calcifuge at sea-level, but occurs on limestones at about 1000 m. and upwards.

Humid climate. In the region of humid climate the rainfall amounts to 1200 mm. or more, but the summer is still always dry though the dry season is shorter than in the other types of Mediterranean climate. The frequent thunderstorms in the mountains have no appreciable effect on the vegetation, which follows a typically Mediterranean rhythm. The mildest, most oceanic type, where it never freezes in winter, is confined to a small area in the extreme north, abutting on the straits of Gibraltar. On the Rif and on the Middle and High Atlas the humid climate is relatively continental, with cold winters. On the High Atlas this climate is represented only by a few small "islands". Though the number of species is less than in the climates mentioned hitherto, nowhere are the forests finer and the vegetation more luxuriant. This is essentially the region of *Cedrus atlantica*, *Abies pinsapo maroccana*, and the deciduous oaks. Forests of maritime pine and of cork and holm oak are also present.

The *Cedretum atlanticae* at its best is a magnificent forest. There are still 200,000 hectares in the Middle and eastern High Atlas and about 15,000 in the Rif, but a great deal has been destroyed. The finest development of cedar forest is in situations fully exposed to the moisture-laden west winds. The cedar descends (exceptionally) to 1350 m. and ascends (with remarkable uniformity) to 2700 or 2800 m., but it never reaches the upper forest limit which is always formed by *Juniperus thurifera*. This behaviour is determined by the cold dry climate characteristic of the high mountains which gives the advantage to the juniper. Where dryness alone limits the cedar it gives way to *Juniperus phoenicea*, *Pinus halepensis*, *P. pinaster*, or *Quercus ilex*. Where humidity increases beyond a certain point the cedar is replaced by deciduous oaks and *Abies pinsapo*. The cedar forests show a number of distinct types, some of which possess a considerable number of west European species besides numerous endemics. Smaller cedar forests occur on the Algerian Tell Atlas and in the Djurdjura. The elevated basaltic plain round Timhadit in the Middle Atlas is now grass-covered, but is said to have been once cedar forest. Both Prof. Stomps (p. 164) and Prof. Osborn (p. 172), however, express scepticism on this point. At present cedar forest is confined to the craters of old volcanoes which form isolated hills arising from the plateau.

Forest of *Abies pinsapo maroccana* is confined to one locality in the western Rif where

it occupies about 15,000 hectares and has an extreme extension from 1300 to 2100 m. of altitude. The fir forest is usually open but may be very dense on northern slopes. It always contains a little cedar and yew, with *Quercus ilex* and *Q. mirbeckii*.

Of the deciduous oaks *Q. toza* forms small pure or mixed woods in the Rif, with *Q. mirbeckii* and also *Q. suber* and *ilex* at its lower, and *Cedrus* at its upper limits. The pure *Quercus toza* forest is in a region of frequent mist, even in summer.

The only other deciduous Moroccan oak is *Q. faginea* (sensu lato) which is a very polymorphic species with three subspecies and several varieties (including "*Q. mirbeckii*") collectively known as "Chêne-Zeem". One or other of these occurs in several places forming pure woods in the Rif and the Middle Atlas, but they are very rare in the High Atlas. These woods are strikingly resistant to invasion by other trees.

Quercus ilex, *Q. suber* and *Pinus pinaster* are the other trees dominating forest in the humid climate. The holm oak woods of this region form lofty closed high forest as above Azrou in the Middle Atlas, with a deep soil rich in humus and abundant mosses and lichens. They contain a number of west European as well as many Mediterranean shrubs and herbs. The humid cork oak woods occur only in the western and central Rif and south-west of Taza. These again are dense closed forests; but the cork oak is near the limit of its humidity tolerance, and the bottoms of the ravines are occupied by the holm oak or by deciduous oaks. The forests of maritime pine in this climate are not pure, the main dominant being associated with fir, cedar, cork oak or holm oak, according to the soil. But in the Middle Atlas there is magnificent dense and nearly pure pine forest with tall and very straight trunks.

High mountain climate. This corresponds with the uppermost mountain zone where trees were never present. The climate is cold and relatively dry. The summer is always dry, just as at lower altitudes, though the total annual rainfall varies a good deal. This climate differs markedly from the alpine climate of central Europe. The highest Rif summits (2450 m.) do not reach into the high mountain climatic zone, which only begins at about 2800–2900 m. This level corresponds with the upper limit of trees which varies from 2800 (western High Atlas) to 3200 m. (eastern High Atlas) in accordance with increasing continentality. The forest limit in the oceanic west is formed by *Quercus ilex*, everywhere else by *Juniperus thurifera*.

The vegetation of the high mountain zone consists of about 350 species, of which more than 100 are endemic, with chamaephytes and hemicyptophytes preponderating and also a number of nano-phanerophytes. It is these last which are physiognomically dominant, many forming characteristic spiny cushions, e.g. *Alyssum spinosum*, *Bupleurum spinosum*, *Arenaria pungens*, *Cytisus balansae* and *Erinacea anthyllis* (the two last endemic), which everywhere characterize this zone. None attains the highest summits, and above 3900 m. there is a population numbering 26 exclusively herbaceous species (19 hemicyptophytes and 7 chamaephytes) very sparsely scattered. No less than 20 are endemic and none is northern, so that the "alpine" vegetation, like the "alpine" climate of Morocco, is very different indeed from that of the high European mountains. Northern species find no suitable habitats among the very dry summits of the High Atlas and are confined to lower slopes where the humid or subhumid climate prevails.

Prof. Stomps contributes a discussion of the vegetational zones of the Atlas, Prof. Regel discusses a number of topics—"steppes", desert, *Quercus ilex* and the tree limit, dunes, oases—raised by his observations of Moroccan vegetation, and Dr R. G. Werner makes some comments on the lower cryptogams, especially on Bryophytes of disjunctive distribution. Prof. Osborn makes an interesting comparison between the vegetation of Morocco and that of southern Australia. The correspondences between the climate, soil and vegetation of certain stations in the two widely separated continents are extremely striking—for example between the climates of Rabat and Adelaide, where the mean maximum and the mean

minimum temperatures as well as the total rainfall and its seasonal distribution are almost identical, the only marked difference being two rainfall maxima at Rabat (November and March) and practically no rain in the summer; while at Adelaide there is a single maximum in June (corresponding with December in the Northern hemisphere) and a monthly 20 to 30 mm. in the summer. The physiognomy of the dominant vegetation is here however unlike, the cork oak contrasting with eucalyptus, but the subordinate layers show considerable resemblances. The detailed correspondence of climate in other pairs of stations is not quite so close, but the type of climate is clearly the same, and some of the vegetational resemblances are remarkable, for example, the similarity of the "shrub steppe" east of Marrakesh with *Atriplex halimus* and *Salsola oppositifolia* and that of South Australia with *Atriplex vesicarium* and *Kochia planifolia*, with numerous annuals in both, and light scrub on shallow stony soils. "Owing to the presence of a large naturalized element from the Mediterranean region in the flora of the agricultural parts of South Australia it frequently happens that the very weeds are the same" in the two countries, that is, wherever a European type of agriculture is practised; but the much longer occupation of Morocco by a much larger population practising primitive methods of cultivation has led to destruction of the natural vegetation over a much bigger proportion of the land, though with very numerous native plants covering the temporarily abandoned "fallows". This indeed is one of the dominant impressions received by a traveller in spring time through the plains and low hills of the semi-arid regions of Morocco—the enormous extent of country which has been cultivated but with existing crops only here and there, and the great abundance of plants, largely annuals, with conspicuous flowers—species of *Anagallis*, *Calendula*, *Chrysanthemum*, *Echium*, *Ferula*, and many others, forming an intricate mosaic of gorgeous colour.

Certain soil correspondences are also marked. In many parts of the arid region near the Atlantic coast of Morocco there is a layer of "travertine limestone"—continuous or as isolated concretions—on or near the surface. This may be interpreted as an illuvial horizon exposed by wind erosion, and Prof. Osborn compares the soils with the "mallee soils" of South Australia in which there is a similar calcareous B horizon.

Dr Lüdi collected an astonishingly large number of specimens of the soil profiles encountered, many of them including samples from considerable depths (50–250 cm.), besides making a number of field observations on the profiles, and of these he contributes a very full account. Podsoils were nowhere met with, but there was a variety of brown earth soils in the more humid regions. By north European standards the pH values run high, many of the brown earths showing alkaline reactions even at the surface, and the few acid reactions met with were very moderate. Marked decalcification by leaching was however found in the regions of higher rainfall, and in general both humus and total carbonate contents were very variable, largely in correspondence with the various nature of the subsoil. In the semi-arid regions the soil type was often "red earth", and evidence was found not only of a calcareous B horizon due to the downward movement of water, but also of a subsurface layer of calcareous concretions resulting from an ascending current. The pH values usually exceeded 8. The soils of the arid region are highly alkaline and commonly show the heavy calcareous "croûtes désertiques" or "travertine limestone" already mentioned.

Lüdi concludes that the whole series of Moroccan soils, from humid to arid, would bear communities of woody plants in the absence of human intervention. He thinks that before the widespread disturbance due to cultivation began the Moroccan soils were in general mature, in equilibrium with all the environmental factors, and occupied by "climax" vegetation, with the implication that the immature soils would be occupied by seral vegetation. The reviewer is of opinion that the underlying assumption of strict parallelism between the development of soil and the development of vegetation is very questionable, since the time factor involved may be of a different order in the two cases. But this is not the place to argue the point. The Moroccan soils which are still immature tend to be dry with

surface accumulation of salts owing to the prevalent high evaporation rates, and over these the more xerophilous vegetation tends to spread, even in the less arid regions. A great part of the country is occupied by soils whose surface layers have been disturbed and altered by tillage; and when these are fallow they are occupied, as we have seen, by ruderal communities, the return of any original vegetation of woody plants being slow and difficult.

A. G. T.

Dundas, J. *Vegetation Types of the Colonie du Niger*. Imperial Forestry Institute Paper, No. 15. 11 pp., 2 plates and 2 sketch maps. Price 3s. 6d.

This paper is a useful contribution to our knowledge of a little-known and misunderstood region, giving a descriptive picture which enables us to place the vegetation in proper perspective in relation to that of the rest of Africa.

The author concludes that the prevailing climate is more humid than it was in the immediate geological past, and that over most of the area the desert sand is now firmly anchored by grass and tree growth.

Several tree species belonging to a higher rainfall vegetation type in Southern Nigeria occur in this semi-desert region under the influence of telluric moisture. No widespread signs were found of recent increase or decrease of Riparian Woodland; this formation is considered by Mr Dundas to be the normal edaphic climax, due to telluric moisture within a different climatic climax.

It is regrettable that the author did not include some details of biotic factors affecting the vegetation—the extent, if any, of the damage by annual fires, shifting cultivation or grazing. In the *Report of the Anglo-French Forestry Commission, 1936–7*, of which Commission Mr Dundas was a member, these factors are dealt with more in relation to the heavily populated areas of Northern Nigeria; it would appear from the paper under review that they are not serious factors in the degradation of vegetation in the Niger Colony, on account of the sparsity of population.

In his last paragraph Mr Dundas draws attention to two old and probably widespread fallacies regarding Riparian Woodland in the Sahelian and Sudanese Zones of Africa: (a) that it is a proof of ecological retrogression, because it is the last remnant of a type of vegetation that once covered the whole area; (b) that it is a proof of ecological progression because it is the advance guard of a more humid type. Mr Dundas agrees with the modern ecological conception of Riparian Woodland as a normal edaphic climax due to telluric moisture.

F. E. HUGHES.

NOTICES OF PUBLICATIONS

EUROPEAN VEGETATION

Stamm, E. *Die Eichen-Hainbuchen-Wälder der Nordschweiz. Beiträge zur geobotanischen Landesnahme der Schweiz, Heft 22.*

The oak-hornbeam woods in the lower parts of the river valleys of North Switzerland are described. The natural position of the true Querceto-Carpinetum is on valley terraces which are not damp enough for alder and not suitable for beech or fir. In regions of high rainfall, this passes into Querceto-Carpinetum fagetosum and on calcareous soil into Q-C calcareum. In damp parts, near the mountains, Q-C alnetosum preponderates, while on light soil, poor in humus, a more acid type of woodland prevails (Q-C acidiphilum). The presence of *Carpinus* wood in neolithic lake-dwellings and of *Carpinus* pollen in the peat shows that this tree was established very early in S.W. Switzerland, while it has always been a component of the forest in historic times. The paper is illustrated by photographs and by maps showing the distribution of the more important elements of the ground flora in Europe and in Switzerland.

Størmer, P. *Vegetationstudien auf der Insel Haøya im Oslofjord. Det Norske Videnskaps-Akademi i Oslo, no. 9. Oslo. 1938.*

This paper describes the vegetation of an island in the Oslofjord. The associations of higher plants are arranged in two groups occurring in a marine and in a more terrestrial environment. A series of transects across the island show the distribution of trees and the relationship of the extent of the tree canopy to the nature of the ground flora. Considerable attention is devoted to the moss vegetation of trees and rocks. Extensive plant lists and a number of photographs accompany the paper.

Goksøyr, H. *Das Pflanzenleben auf Rundøy, Sunmore in Norwegen. Pp. 184, 1 map and 27 text-figures. Det Norske Videnskaps-Akademi i Oslo. 1938.*

A detailed account is given of the plant communities on the island of Rundøy, 30 km. west of Aalesund. Attention is focused mainly on the higher plants though bryophytes and lichens are also noticed. The algal associations are unfortunately not considered. The prevalence of alpine plants usually associated with mountain regions is discussed and it is suggested that, as the island escaped the last glaciation, these may be relics of a pre-glacial flora.

BRITISH VEGETATION

Richards, P. W. "The Bryophyte communities of a Killarney oak-wood." *Ann. Bryologici*, **11**, 108, 1938.

This is an account of the bryophyte communities in Derrycunihy Wood, described in this Journal (1938) by Turner and Watt. Seven habitats are recognised, but it is regarded as probable that the different communities tend to approach a climax community in which certain tall mosses form a closed sward. Three "facies" of the woodland are recognized, varying in exposure and illumination.

Fenton, E. Wyllie. "Surviving remnants of old Scottish forests and their present day value." *Scot. Forest. J.* **52**, 103, 1938.

This is a record of the occurrence of old forests in Scotland, with the author's views of the status of the trees composing them.

POST-GLACIAL VEGETATION

Godwin, H. and Mitchell, G. F. "Stratigraphy and development of two raised bogs near Tregaron, Cardiganshire." *New Phytol.* **37**, 425, 1938.

This paper deals with the detailed structure and the pollen analyses of the peat below a Welsh bog, the vegetation of which is described in the present number (this Journal). In essence, the stratification resembles that known to occur elsewhere in this country and abroad. But no such full account of the detailed stratification of a British moss has previously appeared and the paper is therefore of great importance and its details of great value.

Godwin, H. and Newton, L. "The submerged forest at Borth and Ynyslas, Cardiganshire." *New Phytol.* **37**, 333, 1938.

This paper deals with an example of the submerged forest remains along the west coast of England and Wales. These relics are of considerable interest in relation to the post-glacial history of vegetation, and in the present case the data, collected by the late Mrs Campbell James, deal with the general features and pollen analysis both of the peaty forest deposit and of a closely adjacent peat bog.

Godwin, H. "The origin of Roddons." *Geogr. J.* **91**, 241, 1938.

Roddons are the banks of silt lining the extinct waterways in the Fens. In this paper their origin is discussed and it is shown that they are composed of marine silt, and that the silt banks were formed during the Romano-British period. Pollen analysis of the adjacent peat suggests that it was contemporaneous.

BRITISH ECOLOGICAL SOCIETY

EASTER MEETING

A MEETING of the Society was held at 11 a.m. on Tuesday, 4 April, in the Metallurgical Lecture Room, Imperial College of Science, Prince Consort Road, South Kensington, London, S.W. 7. About 50 members were present.

In the private business which followed the opening of the meeting a recommendation by the Council was approved that a grant of £10 be paid to the Fresh Water Biological Association for the purchase of apparatus for research on lake bottom deposits.

Mr K. R. Sporne was elected a member of the Society.

The President, Prof. A. G. Tansley, F.R.S., then gave his Presidential address on "The present position of British Ecology". Although the President's notes had that morning disappeared, the meeting nevertheless received a very interesting extempore address.

At the conclusion of the President's address Dr G. C. Varley read a paper on "The population density of the knapweed gall-fly". The gall-fly, *Euribeia jaceana*, belongs to the Tripetidae and is particularly useful for census work because it spends its whole life in the single flower head of *Centaurea nigra*. Dr Varley gave an extremely careful analysis of the factors determining population density and attempted to show the percentage losses attributable to different causes in the life cycle; a very important factor is parasitism by hymenoptera, especially *Eurytoma curta*, and it was pointed out that fluctuation in this parasitic attack at different stages of the life cycle might lead to very unexpected results in population density. Other destructive factors of importance were caterpillars and mice. In the discussion which followed Dr Godwin, Dr Turrill and Dr O. W. Richards took part.

After lunch Dr V. J. Chapman gave a very interesting account of the salt-marshes of the British coasts. He made out a generalized scheme of succession for each of four main types which he distinguished. These were (1) the south coast type, which showed deep soft mud and no development of marsh fucoids; (2) the east coast type from the Thames to the Firth of Forth, which showed both sand and mud successions of considerable complexity. This type was characterized by a rich development of marsh fucoids and *Obione portulacoides*; (3) the west coast type on bare sand or sandy mud with *Glyceria maritima* abundant throughout and *Obione* rare. This type is often heavily grazed and shows erosion terraces: it shows very few marsh fucoids; (4) the southern Irish coast type in which the marshes are formed on a "marine peat" formed from remains of the General Salt Marsh. This type, as yet little investigated, has very abundant marsh fucoids. An interesting discussion followed, in which the President, Dr Godwin, Dr Valentine, Mr Tutin, Mr Montford and Miss Gibson took part.

Mr Scott-Russell then gave an account of investigations which he had made during an expedition to Jan Meyen, upon the effect of the arctic environment on metabolic processes involved in plant growth. He rapidly surveyed a very large amount of experimental work dealing in the first place with soil nitrogen and in the second with carbohydrate metabolism. He demonstrated clearly that soil nitrogen is low everywhere, but particularly so on open hill-sides with sparse vegetation. There is a good correlation between improving nitrogen supply, increasing soil population, and increasing vegetational luxuriance.

The net photosynthesis rate was determined at 0.30 mg. per sq. dm. per week for detached leaves of *Oxyria digyna* kept in moist sand. Porometer studies showed that the diurnal rhythm of stomatal movement was kept up in the arctic summer, and analyses showed increasing starch concentrations through the growing season. It was concluded that

carbohydrate synthesis is "adequate for the requirements" of the plants. In the discussion the President, Dr Evans, Mr G. E. Blackman and Dr Watt took part.

Mr G. E. Blackman then gave an account of the relationship of light intensity and the distribution of the bluebell in woodlands. He discussed the results of dry-weight measurements of plants throughout the growing season both in natural conditions and under experimental control. There are three phases in the growth of the plant: (a) in which the total weight alters little, as material is transferred from the bulb to leaves and shoots, (b) a period of rapid growth in April leading to maturation of the seeds, and (c) a final fall in dry-weight. In one season the weight of the whole plant increases about three times and the bulb weight about 60%. The experiment of growing bulbs of uniform weight under conditions of reduced light intensity showed that reducing the light intensity to one-half lowered the growth rate appreciably, and lowering it to a quarter allowed very little increase in bulb weight. It was suggested that about 10% light marked the compensation point, at which no increase in weight could take place. A similar effect was found by planting bulbs of known weight in natural conditions but within containers freeing them from root-competition and lack of water. Much interest was aroused by the paper, and in the discussion the following members took part, the President, Dr Watt, Dr Godwin, Mr Tutin, Mr Montford, Mr Gilmour and Mr Middleton.

The concluding paper of the meeting was read by Mr C. E. M. Tidmarsh on "The significance of morphology in the autecology of *Carex arenaria*". He gave a series of diagrams showing the development of the seedling plant, the evanescent primary root, formation of tillers, the rhizome sympodium, superficial and deep-growing roots and the long and short shoots. He contrasted the different morphology of the plant in eight different soil types, including chalk sand, podsols, and deep unpodsolized sands. In the shallower and the stiffer soils the degree of branching is much lower than in more favourable soils, the greatest cover-percentage and densest branching occurring in closed Caricetum or deep unpodsolized sands. In the shallower soils the deep-growing thick roots, which arise in pairs at the nodes, are restricted by stiff subsoils, and their functional life is limited, the plant becomes dependent upon the superficial roots in the dry upper soil layers, and this proves unsatisfactory. In the following discussion the President, Prof. Gregory, Dr Godwin and Mr Middleton took part.

The President then on behalf of the Society thanked Prof. Brown and the University authorities for allowing the meeting to be held in Imperial College, expressed our gratitude to Prof. Gregory for his encouragement and presence at the meeting, and our warm appreciation to Mr G. E. Blackman for the trouble he had taken in making the arrangements.

H. GODWIN

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